# The Classification of the Papilionidae (Lepidoptera)

*by*

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## Historical Note

The foundation of a natural classification of the Papilionidae was laid in the series of papers by Rothschild (1895), Rothschild and Jordan (1906), and Jordan (1896, 1908-09). In these papers credit is generously given to such predecessors as Felder and Felder (1864) and Haase (1892), who had progressed far towards a correct understanding of the group. However, the unsupported work of the latter men had been ignored or criticized by contemporary authors, whereas the wealth of detailed morphological and taxonomic evidence marshalled by Rothschild and Jordan coupled with the accuracy and insight evident in their work carried immediate conviction, and the arrangement proposed by them 50 years ago has stood virtually unchanged to the present day.

The two main papers by Rothschild and Jordan (1895, 1906) were to have been complemented by a third paper dealing with the African fauna and by a final generic revision, arranging the groups from different regions in a general classification. Unfortunately circumstances prevented this. Aurivillius (1898, 1908-10) independently advanced a classification of the African forms, which has since been modified and improved by Le Cerf (1924) and by Berger (1950, 1951). Forbes (1924), Ford (1941, 1944, 1944) and Zeuner (1943) have made interesting contributions toward an overall classification, but a completely satisfactory subfamily arrangement and generic division have not yet been achieved. I have hoped for some years to complete a thorough generic revision, and have done considerable work toward that end. As it now seems likely that lack of time and material will keep me from further work on this project, I present my conclusions as they stand, fully recognizing that many points of uncertainty or ignorance remain to be resolved.

## Family Papilionidae

The classification of the Papilionidae has always been a source of great difficulty. This is partly because a wide diversity of appearance, life cycle, and habits is to a large extent not reflected in corresponding structural differentiation, and partly because the natural differences that do exist are often obscure and masked by parallelism. The main characters available for grouping are the following: (1) scaling and sensory structures of antennae; (2) structure of palpi; (3) scaling, spining, and pretarsal armature of legs; (4) wing-venation; (5) structure of inner margin of hind wing; (6) wing-pattern and pigmentation; (7) structure of male genitalia; (8) structure of female genitalia; (9) structure and foodplant associations of larva; (10) structure of pupa; and (11) geographic distribution[1]. These characters are of different weights, and have different relative weights in the different groups, so that no purely schematic arrangement is satisfactory. I propose first to discuss the primary division into subfamilies, then to discuss the classification of each subfamily in turn, with emphasis on the most difficult group, the Papilioninae or swallowtails proper.

Ford (1944) recognizes four subfamilies of Papilionidae. Of these, the Zerynthiinae and Parnassiinae differ according to Ford's summary only in the method of pupation and the probably associated rigidity of the pupal abdomen. Although the peculiar pupal structure is a valid grouping character, it is undoubtedly secondary, and the *Parnassius* and *Zerynthia* complexes are otherwise closely allied. Were it not for the pupa we

[1]Some additional integumental characters are discussed by Ehrlich (1958).

should unhesitatingly associate the parnassiine genus *Archon* with the *Zerynthia* complex, in which it rather closely resembles *Allancastria* in wing venation and male genitalia. I therefore unite these two groups in a single subfamily Parnassiinae, of co-ordinate rank with the Papilioninae and the Baroniinae.

The main characters of the three subfamilies are as follows:—

BARONIINAE: antennae very short; radial venation of fore wing reduced; no basal spur from Cu; 2nd and 3rd A of fore wing not stalked; precostal cell of hind wing large; precosta forked; 1st A absent; 3rd A developed as a tubular vein; male genitalia with 9th and 10th tergites well sclerotized, fused, but free from 8th tergite; early stages unknown.

PARNASSIINAE: antennae of moderate length, scaled or unscaled; radial venation of fore wing normal or reduced; basal spur from Cu absent or rudimentary; 2nd and 3rd A of fore wing free, or, rarely, briefly stalked; precostal cell of hind wing large or small, precosta forked or simple; 1st and 3rd A absent; male genitalia with 9th and 10th tergites well sclerotized, free from 8th; larva with red segmental spots or tubercles, primitively on *Aristolochia;* pupa suspended by a girth or with a girth but enclosed in a cocoon on the ground.

PAPILIONINAE: antennae long and slender, scaled or unscaled; radial venation normal or, in one species, reduced; a well-developed basal spur from Cu of fore wing; 2nd and 3rd A of fore wing usually distinctly stalked; hind wing with precostal cell variable; precosta almost always forked; 1st and 3rd A of hind wing absent or rudimentary; male genitalia with ninth and tenth tergites reduced and often immovably articulated with eighth tergite; larva with or without segmental red spots or tubercles; pupa suspended by a girth.

Ford (1944), following Zeuner (1943), misinterpreted the homology of the anal veins of the papilionid hind wing, identifying 2nd and 3rd A of Baroniinae, Pieridae, and other Rhopalocera with 1st and 2nd A of Papilioninae. He therefore did not recognize the primitive character of the presence in *Baronia* of 3rd A, absent or rudimentary in all other Papilionidae. The preservation of this vein suggests that the Baroniinae diverged from the main papilionid stem below the level of any other existing form. The association of $M_2$ with cubitus, the basal approximation of 2nd and 3rd A of the fore wing, and the preservation of the fore-tibial epiphysis mark *Baronia* as a papilionid; the male genitalia, too, are of papilionid rather than pierid type. The short, naked antennae, the loss of one radial and anastomosis of another with Sc, the fusion of male ninth and tenth tergites and loss of socii, and the weakening of the distal portion of the valve, are specialized characters that eliminate *Baronia* from consideration as a papilionid prototype. The relict distribution in western Mexico harmonizes with the primitive and isolated taxonomic position of the Baroniinae. Although Bryk's (1913, 1934) ranking of the group as a family does not violate taxonomic facts, it does tend to obscure rather than to clarify relationships, and I accordingly follow Ford in retaining the Baroniinae in the Papilionidae as a subfamily. The early stages of *Baronia* are unknown. It will be interesting to see whether or not the larva has an osmaterium and red segmental tubercles, and whether the pupa is suspended by a girth.

The Parnassiinae are definitely more advanced than the Baroniinae in having lost 3rd A of the hind wing. The parnassiine prototype has: scaled antennae and legs; all radials present; 2nd and 3rd A of fore wing approximate, but not stalked; male genitalia with ninth segment free from eighth, and tenth tergite bifid; sphragis present; red-tuberculate, *Aristolochia*-feeding larva; and suspended pupa. The presence or absence of a tail on the hind wing is so unstable a character throughout the family that it is impossible to say whether an actual tail or the tendency to tail-production was a primitive character of Parnassiinae. There is no doubt that the group was originally derived from a tailless form; moreover, the two known Tertiary fossils of the group

lack tails, and the Baroniinae are tailless. On the other hand, the Papilioninae have the same tendency to tail-formation, suggesting that this was a character of the common ancestor of the two subfamilies.

The relationship between the Parnassiinae and the Papilioninae is not entirely clear. There are definite points of resemblance between the Parnassiinae as a whole and certain Papilioninae. The most important are the red-tuberculate larva, the aristolochiaceous food-plant, and the presence of a sphragis. All these characters are likewise found in primitive members of the papilionine tribe Troidini. However, all Troidini have a peculiar and specialized type of male genitalia, in which the ninth and tenth tergites are reduced and closely fused with the eighth tergite and the sclerotized eighth-ninth intersegmental region. Such a condition hardly suggests a direct relationship, either of ancestry or of descent, to the Parnassiinae, which always have the ninth and tenth segments free and exceptionally strongly sclerotized. Another papilionine tribe, the Leptocircini, not only has much more primitive genitalia, with free, and in some genera normally developed, ninth and tenth tergites, but also retains the scaling of antennae and legs which are lost in Troidini. If the morphological homogeneity of the Papilioninae is trustworthy evidence of direct relationship, we must assume that the Troidini are descended from the Leptocircini, though no doubt from forms more primitive than any now living. Most Leptocircini have smooth or few-spined green larvae, feeding on Lauraceae or Anonaceae, and it is noteworthy that at least two other primitive families of butterflies, the Pieridae and the Hesperiidae, include forms with smooth green larvae feeding on Lauraceae, whereas no other primitive butterflies have red-tuberculate larvae that feed on Aristolochiaceae. On the other hand, the larva of *Lamproptera*, a leptocircine genus with primitive genitalia, is described as being like that of *Zerynthia* (Moore, 1902)[2] and as feeding on Combretaceae (Wm. T. M. Forbes, in litt.), also the food of the troidine *Parides antenor*.

Two basic interpretations are possible: either the green Lauraceae-feeding larva is primitive, and the red-tuberculate *Aristolochia*-feeder is a secondary derivative; or the red-tuberculate larva is primitive within the family, and the green larva is a secondary derivative. Each alternative has two variants: if the Lauraceae-feeding larva is primitive, then the Parnassiinae, the Troidini, and possibly *Lamproptera*, may have developed the red-tubercled larva independently (Fig. 1A) — perhaps as an aposematic adaptation — on transferring to Aristolochiaceae, or these groups may all represent branches of a single *Aristolochia*-feeding stock (Fig. 1B); if, on the other hand, the *Aristolochia*-feeding larva is primitive, either the Troidini may have developed independently of the Parnassiinae from a stock near the base of the Papilioninae (Fig. 1C), or they may have developed in close association with the Parnassiinae (Fig. 1D), the resemblances to Papilionini and Leptocircini being the result of convergence.

Present evidence does not show conclusively which type of larva is primitive. The general resemblance of the green, somewhat slug-shaped larva to that of Hesperiidae, Pieridae, and primitive Nymphalidae is striking, and the sharing of the lauraceous food-plant is suggestive. On the other hand, the recurrence of the red-tuberculate larva in three different groups, and the presence of segmental spiny tubercles or red spots here and there in groups with green larvae might be taken as evidence of the alternative view that the red-tuberculate larva is primitive. Discovery of the early stages of *Baronia* may well be decisive, as the Baroniinae undoubtedly arose from a point below the separation of the lauraceous and the aristolochiaceous feeders. Rigorous comparative anatomical study of a wide range of papilionid larvae is desirable too, and might show that some apparent resemblances are superficial. Lack of material has made this impossible at present.

[2]Mr. Kent H. Wilson (in litt.) informs me that this description is erroneous. He has kindly called my attention to the description and figure by Mell (1937:340, Pl. 7, Figs. 9, 18). Plates 7 and 8 in Mell are transposed with respect to the legends.

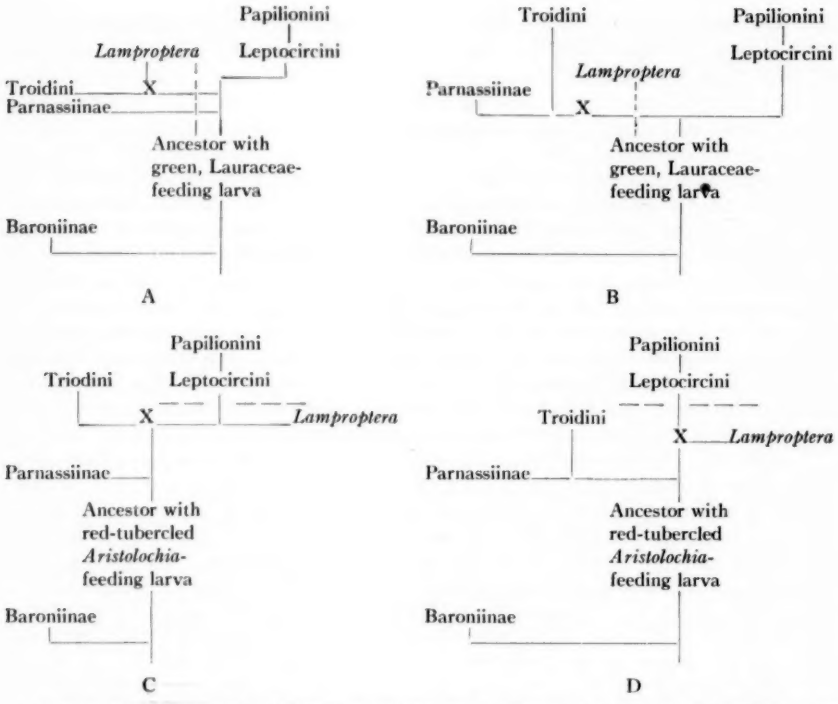


Fig. 1 (A-D).—Possible phylogenies of the subfamilies and tribes of Papilionidae. In each diagram the broken line represents the boundary line between forms feeding on Aristolochiaceae, Combretaceae, and derivatives, and those feeding on Lauraceae and derivatives. "X" is a hypothetical unspecialized ancestor of *Lamproptera*. "Leptocircini" means the Lauraceae-Anonaceae-feeding wing of the tribe only.

## Subfamily Baroniinae

Baroniidae Bryk, 1913: 116.

Head wide; antenna very short, naked; palpus short, third joint longest. Legs scaled, fore-tibial epiphysis present. Fore wing with $R_1$ anastomosing with Sc, $R_4$ lacking $R_3$ stalked with $R_{4+5}$; 2nd and 3rd A diverging from base. Hind wing with precosta forked, precostal cell long, 1st A lacking, 2nd and 3rd A well developed.

Wing pattern simple and probably primitive. Ground-colour dark, with extensive pale basal areas, and with two rows of pale submarginal spots, the inner row divided on costal half of fore wing.

Male genitalia: ninth segment freely movable on eighth; vinculum narrow; sacculus moderate; tegumen and uncus well sclerotized, completely fused; valve with stout base produced into a thorn-like clasper; distal portion of valve weakly sclerotized, setose; aedoeagus simple and almost straight.

Female genitalia not examined.

### Genus *Baronia* Salvin, 1893

**Type-species: *Baronia brevicornis* Salvin**

Characters as for the subfamily. The genus is monotypic. The single species is known only from Guerrero, Mexico.

## Subfamily Parnassiinae

Parnassii Latreille, 1802: 395.

Though the genera of this subfamily are all plainly related, they show considerable aggregate structural variation. General build moderately robust, with body short but hairy and fairly stout. Head with palpus and antenna variable in shape, the latter scaled or naked, with or without ill-defined ventral sense-pits. Scales often reduced in size, rendering the wing transparent or translucent. Markings composed of fairly regular bands or rows of spots, often black, the basal and postmedial bands often containing red pigment "A" of Ford. These red-centred bands reappear in the graphiine Papilioninae. The red spots of Troidini, though similar chemically, are apparently not homologous as pattern elements.

The following can be postulated as characters of the parnassiine prototype: head broad; antenna scaled; palpus moderately short, porrect or obliquely ascending; tibiae and tarsi scaled; claws simple, equal, not sexually dimorphic; fore wing with all radials present, $R_3$ from angle of cell, $R_{4+5}$ stalked, median spur present, though perhaps reduced, 2nd and 3rd A not stalked; hind wing rounded, possibly with a tail at $M_3$, probably with an excavation on anal margin near anal angle, precostal cell large and precostal vein forked; pattern consisting of mid-cellular and discocellular black bars on fore wing, discocellular bar on hind wing, a basal and a postmedial dark band, probably with intervenular red spots at least beneath, a black mesial band between mid-cellular and discocellular spots of fore wing, and two dark bands or rows of spots or lunules parallel to or immediately preceding outer margin, the inner of these rows probably dusted with blue scales; male genitalia with normal eighth tergite, narrow, free ninth segment, well sclerotized tegumen and uncus, the latter bifid (these processes possibly really the socii), valve narrow, with heavily sclerotized base, continued as a strong, unmovable, hook-like clasper; female with a sphragis; larva cylindrical, dark-coloured, with low, red segmental tubercles, feeding on *Aristolochia;* pupa suspended by a girth.

Table I classifies the eight genera of Parnassiinae in terms of their fidelity to the prototype in 19 presumably independent characters. The condition in each genus has,

TABLE I
*Primitive or Specialized Condition of Nineteen Characters in Parnassiine Genera*

| | Archon | Hyperm-nestra | Par-nassius | Zeryn-thia | Allan-castria | Sere-cinus | Lueh-dorfia | Bhu-tanitis |
|---|---|---|---|---|---|---|---|---|
| Antennal Scaling | p | p | p | s | s | s | s | s |
| Palpi | p | p | p | p | p | s | p | p |
| Leg Scaling | p | p | p | s | s | s | s | s |
| Tarsal Claws | s | p | s | s | s | s | s | s |
| R: | s | s | s | s | s | p | s | s |
| R; | p | s | s | p | p | p | p | p |
| Median Spur | s | s | s | s | s | p | s | p |
| 2nd & 3rd A | p | p | p | s | p | p | p | p |
| Pattern | p | p | s | p | p | p | s | s |
| ♂VIII Tergite | p | p | s | p | p | p | p | p |
| ♂IX & X Tergites | p | p | s | p | p | p | p | p |
| Valve | s | s | p | s | s | s | s | s |
| Sphragis | p | p | p | | | | p | p |
| Larva | p | p | p | p | p | p | s | p |
| Food-plant | p | s | s | p | p | p | p | – |
| Pupa | s | s | s | p | p | p | p | – |
| Precostal Cell | s | s | s | p | s | p | s | p |
| Precostal Vein | s | s | s | s | s | p | p | s |
| Wing Shape | p | p | p | p | p | s | s | s |

in some cases rather arbitrarily, been entered as primitive (p) or specialized (s). The number of specialized characters shown by a genus gives some idea of its status, though the characters naturally do not all have the same weight. The two tribes are set off sharply in antennal and leg scaling and in mode of pupation. Though *Serecinus* in the Zerynthiini has the largest number of primitive characters, some of these are of minor significance. The Parnassiini cannot have been derived from *Serecinus* or any other existing zerynthiine, for the Parnassiini all have normally scaled legs and antennae, a condition more primitive than that of the Zerynthiini, in which these organs are unscaled. The specializations of *Archon* are in fact slight; the pattern shows some highly primitive features — notably the presence of a complete row of red postmedial spots on both fore and hind wings — and the genus is probably not far removed from the common ancestor of the two tribes. It should be noted that, though the terrestrial, cocooned pupa is here considered a secondary development, a similar pupation habit is found in the Hesperiidae. In the absence of information on the pupal habits of *Baronia*, the terrestrial pupa could be interpreted as primitive, and the suspended pupa of Zerynthiini and Papilioninae as specialized. This would lower the relative position of *Archon* in Table I and raise that of *Serecinus*.

### Tribe Parnassiini

Ford's interpretation of relationships in this group seems satisfactory. *Archon* is primitive, *Hypermnestra* is close to *Parnassius*, but more primitive in minor respects. The tribe as a whole is distinguished by the scaled antennae and legs and by the terrestrial pupa.

### Genus *Archon* Hübner
### Type-species: *Papilio thia* Hübner

*Archon* Hübner 1822: 2.

More primitive than other members of the tribe in preserving all five radials of the fore wing and in retaining *Aristolochia* as the food-plant. The single species occurs in Thrace and Asia Minor.

### Genus *Hypermnestra* Ménétriés
### Type-species: *Ismene helios* Nickerl

*Ismene* Nickerl 1846: 207, *nec* Savigny, 1816, Swainson, 1820, *nec* Stephens, 1834. Type-species: *Ismene helios* Nickerl.
*Hypermnestra* Ménétriés, 1851: 84B.

Similar to *Parnassius* in most structural features: precostal vein bent distad, not basad; pattern less strongly reduced; male eighth tergite not produced in large postero-ventral flaps; sphragis small. The single species occurs in steppe or desert lands from northern Persia to Turkestan and Baluchistan. Larva on *Zygophyllum*.

### Genus *Parnassius* Fabricius
### Type-species: *Papilio apollo* Linnaeus

$R_4$ of fore wing lost, $R_3$ stalked with $R_{4+5}$. Wings rounded, pattern reduced to an extent variable with species and sex. The most extensively marked forms with pattern consisting of black mid-cellular and discocellular spots on fore wing and three dark or hyaline bands or rows of spots on each wing beyond cell; first post-cellular band of hind wing incomplete above, usually consisting of black-rimmed red spots in cells Sc and $M_1$, sometimes with additional dark or red spots; second postcellular band of hind wing consisting in many species of round, blue, black-rimmed spots. Under side of hind wing with red basal and post-cellular bands well developed. Male genitalia variable, but always with eighth tergite prolonged into ventro-posterior flaps; female after copulation with a prominent sphragis. Larva red-spotted, on low plants. Distribution montane and northern in the Palaearctic and western Nearctic regions.

Bryk (1935) divides *Parnassius* of authors into five genera, on the basis of (a) anastomosis or non-anastomosis of $R_2$ with $R_1$, (b) point of origin of $M_1$, and (c) relative length of fore-tibial epiphysis. The groups so defined do not agree very well with natural groups as indicated by male genitalia: what appears to be the main cleavage, between the *apollo* group on the one hand and the *mnemosyne* group and the four remaining "genera" on the other, is obscured. I think the *stoliczkanus* group of *Koramius* is more closely related to the *imperator* group of *Tadumia*, and the *szechenyii* group of *Koramius* to the *acco* group of *Tadumia* than is the *stoliczkanus* group to the supposedly congeneric *szechenyii* group and the *imperator* group to the *acco* group. The species *simo* G. R. Gray and *tenedius* Eversmann, referred by Bryk to *Tadumia*, both have aberrant genitalia, and are not closely related to one another or to the other species placed in the genus. The *apollo* group and the *mnemosyne* group appear to represent divergent primitive strains; the remaining groups can be regarded as direct or indirect derivatives of the *mnemosyne* group.

As the division based on external characters is unnatural, and as the group is an extremely homogeneous one in ecology and general habitus, I prefer to include all the forms in one genus. It is probably useful to recognize two subgenera: *Parnassius*, with a spatulate process (uncus?) between the two lateral processes (socii?) of the male tenth abdominal segment, and *Doritis*, without such a central process.

### Subgenus *Parnassius* Fabricius

*Parnassius* Fabricius, 1775: 465.
*Therius* Billberg, 1820: 77. Type-species: *Papilio apollo* Linnaeus.

$R_2$ not anastomosed with $R_1$; fore-tibial epiphysis not reaching end of tibia; male with a spatulate process between the two thorn-like processes of the tenth tergite; valve narrow, with rounded tip and clasper broad at base; eighth tergite of male with anterior and lateral margins forming a single arc, posterior extremities rounded, posterior emargination deep and circularly expanded; sphragis posteriorly flat and leaf-like; hind wing never with blue spots. One group of ten species; Palaearctic and Nearctic.

### Subgenus *Doritis* Fabricius
### Type-species: *Papilio mnemosyne* Linnaeus

*Doritis* Fabricius, 1807: X.
*Tadumia* Moore, 1902: 116. Type-species: *Parnassius acco* G. R. Gray.
*Kailasius* Moore, 1902: 118. Type-species: *Parnassius charltonius* G. R. Gray.
*Koramius* Moore, 1902: 120. Type-species: *Doritis delphius* Eversmann.
*Lingamius* Bryk, 1932: 1. Type-species: *Parnassius hardwickei* J. E. Gray.
*Eukoramius* Bryk, 1934: 43. Type-species: *Parnassius imperator* Oberthür.

$R_2$ free or anastomosed with $R_1$; fore-tibial epiphysis of varying length; tenth tergite of male ending in a pair of pointed processes, or, rarely, in a single truncate process; valve and clasper various; eighth tergite of male often with sharp anterolateral angles, when such angles absent and a rounded posterior emargination present the margination not circularly expanded; sphragis scoop-shaped, often very large; blue-centred subterminal spots present in one or more species of most of the groups.

*Mnemosyne* group: $R_2$ arising from cell, not anastomosing with $R_1$; $M_1$ from cell or stalked with $R_{2-5}$; fore-tibial epiphysis not reaching end of tibia. Uncus bifid, with paired dorsal processes; valve distally emarginate, longest ventrally; female eighth tergite with trapezoidal emargination, anterior angles well defined. Seven species; Palaearctic and Nearctic.

*Hardwickei*-group: $R_2$ arising from cell, not anastomosing with $R_1$; $M_1$ stalked with $R_{3-5}$; fore-tibial epiphysis reaching end of tibia. Uncus bifid, with paired dorsal processes; valve distally emarginate, dorsal flange and ventral point about equal in length; female eighth tergite with subquadrate emargination, anterior angles well defined. One species; Palaearctic.

*Szechenyii*-group: $R_2$ arising from cell, not anastomosing with $R_1$; $M_1$ from cell; fore-tibial epiphysis reaching end of tibia. Uncus bifid, with paired dorsal processes; valve distally entire, ventral angle developed; female eighth tergite with rounded emargination, anterior angles well defined. Two species; Palaearctic.

*Acco*-group: $R_2$ arising from cell, anastomosing with $R_1$; $M_1$ from cell; fore-tibial epiphysis reaching end of tibia. Uncus bifid, without dorsal processes; valve distally entire, ventral angle obtuse; female eighth tergite with deep, rounded emargination, anterior angles rounded off. Five species; Palaearctic.

*Delphius*-group: $R_2$ from cell, not anastomosing with $R_1$; $M_1$ from cell; fore-tibial epiphysis reaching end of tibia. Uncus bifid, without dorsal processes; valve with distal margin oblique, ventral angle suppressed; female eighth tergite with shallow, rounded emargination, anterior angles well marked. Five species; Palaearctic.

*Imperator*-group: $R_2$ from cell, anastomosing with $R_1$; $M_1$ from cell; fore-tibial epiphysis reaching end of tibia. Uncus bifid and laterally emarginate; valve with distal margin oblique, ventral angle suppressed; female eighth tergite with deep, rounded emargination, anterior and posterior angles well marked. One species; Palaearctic.

*Charltonius*-group: $R_2$ stalked with $R_{3-5}$, anastomosing with $R_1$; $M_1$ from cell; fore-tibial epiphysis reaching end of tibia. Uncus bifid; valve with distal margin rounded; female eighth tergite with deep, triangular emargination, anterior and posterior angles rounded off. Three species; Palaearctic.

*Tenedius*-group: $R_2$ from cell, anastomosing with $R_1$; $M_1$ from cell; fore-tibial epiphysis reaching end of tibia. Uncus very long, weakly bifid; valve long, slender, distally rounded; female eighth tergite with triangular emargination, anterior angles well marked, posterior angles rounded off. One species; Palaearctic.

*Simo*-group: $R_2$ from cell, anastomosing with $R_1$; $M_1$ from cell; fore-tibial epiphysis reaching end of tibia. Uncus simple, truncate; valve narrow, pointed, claw-like; female eighth tergite hardly emarginate, anterior angles rounded off, posterior angles acute, directed ventrad. One species; Palaearctic.

### Tribe Zerynthiini

Thaidi Tutt, 1896: 84.
Luehdorfiidi Tutt, 1896: 84.
Zerynthianae Grote, 1899: 17.

The generic name *Thais* is a homonym, and is not available as the basis of a tribal name, although Thaidi is the oldest name for the tribe, and the one selected by the first reviser. It must be supplanted by Zerynthiini, based on the valid synonym of *Thais*. This outcome is in harmony with current usage. The Zerynthiini are more specialized than the Parnassiini in having lost much or all of the scaling of antennae, tibiae, and tarsi. The absence of anthoxanthins is regarded by Ford as a specialization, but there is an at least equally good case for considering it primitive. The existing Zerynthiini comprise five rather widely separated genera. The erratic distribution of primitive characters in these genera and the individual nature of their specializations suggest that they have to a large extent radiated independently from an ancestral stock perhaps not very different from *Archon*. In this connection the close resemblance in genitalia and wing-venation between *Allancastria* and *Archon* should be noted. However, as other genera retain primitive features lacking in *Allancastria* — a rudimentary medial spur in *Serecinus* and *Bhutanitis*, and a sphragis in *Luehdorfia* and one species of *Bhutanitis* — *Allancastria* cannot qualify as an ancestral genus. Genitalic structure suggests a fairly close relationship between *Serecinus* and *Zerynthia; Serecinus* is the more primitive in five features of wing-venation. Genitalia, wing-form, and pattern all suggest that *Bhutanitis* is highly specialized, but recent discoveries show clearly its derivation from *Luehdorfia*.

### Genus *Allancastria* Bryk
### Type-species: *Thais cerisyi* Godart

*Allancastria* Bryk, 1932: 104.

Fore wing with $R_3$ short-stalked with $R_{4+5}$, $M_1$ arising at upper angle of cell, discocellular incurved, 2nd and 3rd A not stalked; hind wing with precosta unbranched, curved basad, precostal cell narrow, margin toothed, most strongly at $M_3$; male genitalia with uncus long, bifid, valve simple, lanceolate; female without sphragis. This genus differs in a number of important characters from *Zerynthia* and it is surprising that it was not separated until 1932.

One polytypic species, occurring in the Balkans and Asia Minor.

### Genus *Serecinus* Westwood
### Type-species: *Papilio telamon* Donovan

*Serecinus* Westwood, 1851: 173.

Fore wing with $R_3$ from cell, $M_1$ from upper angle of cell, $M_2$ widely separated from $M_3$ and strongly curved at base, 2nd and 3rd A not stalked; hind wing with precostal vein long, forked, precostal cell very wide, a long tail at $M_3$; male genitalia with uncus short, bifid, with paired dorsal processes, valve broad and ornate; sphragis lacking. One species, in China and Korea.

### Genus *Zerynthia* Ochsenheimer
### Type-species: *Papilio polyxena* Schiffermüller and Denis

*Thais* Fabricius, 1807: XI, *nec* Bolten 1798. Type-species: *Papilio hypsipyle* Fabricius.
*Zerynthia* Ochsenheimer, 1816: 29.

Fore wing with $R_3$ stalked with $R_{4+5}$, $M_1$ arising well below upper angle of cell, median spur absent, 2nd and 3rd A stalked; hind wing with precostal vein simple, precostal cell very narrow, tail lacking; male genitalia with uncus very short, valve broad, irregular, with a strong spine. Two species; Mediterranean region.

### Genus *Luehdorfia* Crüger
### Type-species: *Luehdorfia eximia* Crüger

*Luehdorfia* Crüger, 1878: 128.

Wings as in *Allancastria*, but with precostal vein forked, with tail at $M_3$ definite and points at other veins small, and with a strong indentation in anal margin at anal angle. Male genitalia with uncus long, bifid; valve mitten-shaped, with a prominent mesoventral zone of stout spinules. The pattern of this genus shows mild pierellization, as is not uncommon where well-marked transverse stripes are developed.

Bryk recognizes two living species, both from the eastern Palaearctic region. The extinct *L. bosniackii* (Rebel), from the Miocene of Tuscany, lacks diagnostic characters, and is placed here only as a matter of convenience.

### Genus *Bhutanitis* Atkinson
### Type-species: *Bhutanitis lidderdalei* Atkinson

*Armandia* Blanchard, 1871: 809, *nec* Filippi, 1861. Type-species: *Armandia thaidina* Blanchard.
*Bhutanitis* Atkinson, 1873: 570.

Fore wing with $R_3$ stalked with $R_{4+5}$, $M_1$ from upper angle of cell, precostal spur indicated, 2nd and 3rd A not stalked; hind wing with precostal vein simple, bent basad, precostal cell wide, tails at $M_3$, $Cu_1$ and $Cu_2$; male genitalia with long bifid uncus, valve bulging outward, the whole comprising a heavily-sclerotized, barrel-shaped structure. Sphragis small or absent.

Two remarkable discoveries in recent years have raised the number of known species to four, all from the Sino-Himalayan region. *Bhutanitis mansfieldi* (Riley), new combination, is the most primitive, the wing-proportion, maculation, anal emargination, and retention of the sphragis all being reminiscent of *Luehdorfia*.

## Subfamily Papilioninae

Papilionides Latreille, 1807: 187.

I make no attempt to reproduce the synonymy of this well-established name.

I recognize three tribes in this subfamily: Leptocircini (=Graphiini), Papilionini, and Troidini. *Euryades* and *Cressida* are troidine in every essential respect, and I see no warrant whatever for recognizing them as a separate tribe. *Teinopalpus* has genitalia closely similar to those of primitive Leptocircini; therefore, despite its specializations, I place it in that tribe.

There is no doubt whatever as to which tribe is the most primitive: the primitive Leptocircini have male genitalia of the normal type, with distinct tegumen and uncus, telescoping freely within the eighth abdominal segment. The tegumen and uncus degenerate within the tribe; in the highest forms only the paired socii remain as vestiges of the dorsal part of the ninth and tenth segments, and the ninth segment is firmly articulated dorsally with the eighth tergite, the inter-segmental region being sclerotized and produced. The specialized condition is universal in the other two tribes, though it is achieved in a slightly different way in each. That is to say, the Leptocircini cannot conceivably have been derived from either of the other tribes, whereas both of the other tribes may well have arisen from the Leptocircini. In addition to the genitalia, the scaled antennae and legs of Leptocircini are obviously primitive.

The more precise relationships of the tribes are problematical. Several features point to a direct derivation of the Papilionini from the Leptocircini. The presence of a spineless, impressed space between the dorsal and ventral rows of tarsal spines in both Leptocircini and Papilionini and the sharing of the lauraceous food-plant in primitive forms of both tribes are perhaps the most significant connecting links. However, there is a resemblance in fundamental plan of male genitalia between the leptocircine genus *Dabasa* and the Papilionini; the pattern of the *Papilio glaucus* group and of *P. alexanor* are *Graphium*-like; and the larval and pupal facies of the two groups are not hard to harmonize. Red pigment B, characteristic of Papilionini, occurs in the leptocircine *Iphiclides podalirius*, but is found also in the troidine genus *Battus*. The main arguments against a direct descent of Papilionini from Leptocircini are: (1) though the tuberculate red-spotted larva may be primitive in Papilionini, few Leptocircini are known to have such larvae; and (2) adults of Papilionini resemble those of Troidini in some ways, and might therefore be thought to have evolved from them. Of these resemblances, the more striking are: (a) the Papilionini share the red pigment B with the troidine genus *Battus;* and (b) the male ninth and tenth tergites have degenerated in both groups, the ninth segment has become dorsally attached to the eighth, and a false uncus has been developed on the eighth segment. However, each of these characters occurs also in one or more genera of Leptocircini, and they therefore cannot be used to prove a closer relationship of the Papilionini to the Troidini than to the Leptocircini. On the whole the special resemblances of the Papilionini and Leptocircini seem to leave little doubt of their direct relationship. The only point open to serious debate in whether the Papilionini arose from Leptocircini such as *Iphiclides* or *Dabasa* in which the ninth and tenth segments were already reduced, or whether they arose directly from primitive Leptocircini and acquired this specialization independently, as the Troidini must have done. The primitive, band-like signum of Papilionini, quite different from the horn-like signum of higher Leptocircini, makes a derivation from primitive forms the more probable.

### Key to the Tribes

1. Tibiae and tarsi scaled ..... Leptocircini
   Tibiae and tarsi unscaled ..... 2
2. Tibiae and tarsi with ventral rows of spines separated from dorsal rows by an impressed spineless space ..... Papilionini
   Tibiae and tarsi with ventral rows of spines not separated from dorsal rows by an impressed spineless space ..... Troidini

## Tribe Leptocircini

Leptocircinae Kirby, 1896: 307.
Teinopalpidae Grote, 1899: 16.
Graphiini Ford, 1944: 213.

Antenna scaled, except in *Teinopalpus;* tibiae and tarsi scaled, with the four ventral rows of spines separated by a spineless space from the dorsal spines, which are arranged in fairly regular longitudinal rows. Male genitalia with ninth and tenth abdominal segments weakly sclerotized, retractable except for the valves within eighth segment; region between eighth and ninth segments wholly membraneous except in *Dabasa*. Mature larva in most species green or greenish, usually smooth or with single pairs of conical spines on one or more thoracic segments and on the terminal abdominal segment; rarely with more numerous segmental tubercles or with red spots. Pupa usually smooth, green or brown with two pairs of raised lines extending from cremaster to the thoracic notum, usually ending there in a raised horn; cephalic horns less regularly present. Most species on Anonaceae, but some on Lauraceae, and a few on plants of other families — *Iphiclides podalirius* on Rosaceae, and *Lamproptera* spp. on Combretaceae.

The course of evolution in this tribe is fairly plain. Primitive forms had male genitalia with well-developed ninth and tenth tergites, the tenth tergite being bifid as in *Lamproptera* or trifid as in *Teinopalpus* and *Eurytides*. The pattern and wing-shape were perhaps of the barred "kite" type so common in existing forms. The division into a group with red-tubercled *Aristolochia*-feeding larvae and one with green Lauraceae-feeding larvae was probably early. The former presumably gave rise to the Troidini. Most living genera and species belong to the Lauraceae-feeding stock, which has given rise also to the Papilionini. In this branch of the Leptocircini the most primitive genitalic structure is retained by *Teinopalpus*, but this genus, like *Lamproptera*, is aberrant in adult structure. The main line of evolution is represented more accurately by the Neotropical Leptocircini, all of which I refer to the single genus *Eurytides*. *Eurytides* has the uncus well developed, forming with the socii a trifid structure (except in *E. celadon* (Poey), in which the socii are aborted); where unmodified by mimicry the facies is that of the typical kite-swallowtail, and the veins anastomose or fuse in only a few species. Leaving *Teinopalpus* and *Lamproptera* out of consideration, only one Old-World leptocircine species, the Australian *leosthenes*, has the tenth tergite so well developed. In all the rest the uncus is vestigial or absent, the more or less well-developed socii being separated by a median membranous area. These more specialized forms must have developed from ancestors of the *leosthenes* or *Eurytides* type, which they have largely supplanted in the Old World. Of these higher Leptocircini five species, of the *podalirius* and *payeni-gyas* groups, have the radials free: all the others have $R_1$ anastomosed with Sc. The species *payeni* and *gyas* differ widely from other Leptocircini in the shape of the cell and discocellulars of the fore wing and in various features of the male genitalia. They belong to the very distinct genus *Dabasa*. *Podalirius* resembles the other higher graphiines more closely, but differs in the lanceolate male valve armed with a simple clasper, in the red-spotted, Rosaceae-feeding larva, and in the shape of the pupa. These characters seem to me sufficient for the generic separation of *podalirius* (and presumably the Tibetan *podalirinus*, which I have not examined) from the remaining forms with aborted uncus, which I unite in the large and varied genus *Graphium*. This genus includes: (1) the comparatively primitive *eurypylus*, *agamemnon*, and *sarpedon* groups in Asia; (2) a superficially varied but structurally homogeneous intermediate complex comprising all the African species; and (3) the highly specialized *antiphates* and *macareus* groups in Asia. Comparison of the male genitalia makes the evolutionary progression from 1 to 2 to 3 obvious.

## Key to the Genera of Leptocircini

1. Antennae unscaled, palpi large and porrect ..... *Teinopalpus*
   Antennae dorsally scaled, palpi small and upturned ..... 2
2. Upper discocellular much shorter than middle discocellular ..... *Dabasa*
   Upper discocellular at least as long as middle discocellular ..... 3
3. Fore wing less than twice as long as antenna; $R_3$ stalked with $R_4$ to beyond origin of $R_5$; hind wing with a broad tail much longer than main part of wing ..... *Lamproptera*
   Fore wing more than twice as long as antenna; $R_3$ not stalked with $R_4$; hind wing tailless or with a slender tail rarely as long as main part of wing ..... 4
4. Uncus of male well developed; New World and Australia; Australian species with $R_1$ free ..... 5
   Uncus of male vestigial or absent; Old World; Australian species with $R_1$ anastomosed with Sc. ..... 6
5. Socii fused with uncus to form a well-sclerotized trifid, or rarely simple, structure; New World ..... *Eurytides*
   Socii distinct from uncus; Old World ..... *Protographium*
6. $R_1$ free from Sc ..... *Iphiclides*
   $R_1$ anastomosed with Sc ..... *Graphium*

### Genus *Lamproptera* G. R. Gray
### Type-species: *Papilio curius* Fabricius

*Lamproptera* G. R. Gray, 1832, pl. 102.
*Leptocircus* Swainson, 1833, pl. 106.
*Lamprosura* Moore, 1902: 133.

Antenna dorsally scaled; tibiae and tarsi scaled, dorsal and ventral rows of spines separated by an impressed spineless space; tarsal claws bifid in one species. Fore wing and costal region of hind wing reduced, tail broadened and lengthened. Fore wing with $R_1$ from before middle of cell, $R_2$ from cell, $R_3$ and $R_4$ long-stalked, $R_5$ arising from $R_{3+4}$ just beyond cell; discocellulars in line, upper angle of cell acute, lower angle broadly obtuse; median spur well marked; 2nd and 3rd anals not stalked. Hind wing with precosta simple, precostal cell large, discal cell very small, hardly larger than precostal cell; male with scent-organ in anal fold. Male with eighth tergite normal; genitalia with fully developed and distinct tegumen, and with broad, short, emarginate uncus, fused laterally with socii; valve ovate, with mitten-shaped clasper; aedoeagus weakly decurved, ventro-laterally flanged. Female genitalia not examined.

Larva described as *Zerynthia*-like (Moore, 1902);[3] food-plants: *Combretaceae*.

Two species; Indo-Malayan.

### Genus *Teinopalpus* Hope
### Type-species: *Teinopalpus imperialis* Hope

*Teinopalpus* Hope, 1843: 131.
*Teinoprosopus* Felder and Felder, 1864: 289. Type-species: *Teinopalpus imperialis* Hope.

Frons with rounded or conical prominence; palpus long, thickly scaled; antenna naked. Fore wing with $R_3$ from just beyond angle of cell, $M_1$ from near upper angle, middle discocellular strongly concave outwards, median spur very weak. Hind wing with precosta forked, precostal cell large, 1st and 3rd A lacking, no special development of anal area in male. Tibiae and tarsi scaled, with dorsal and ventral spined areas separated by an impressed spineless space. Eighth abdominal tergite of male with a strongly sclerotized pseuduncus; ninth segment freely retractable within eighth; valve rounded, with a simple, rounded clasper; uncus and socii fused to form a trilobed structure. Female genitalia not studied.

Larva green, papilioniform, with large head. Pupa smooth, green, with a distinctive horn. Food plant *Daphne* (Thymeleaceae, a laurel-like plant).

Probably two species. Range: Sikkim, Assam, Burma, and southern China.

[3]But see footnote [2], p. 7, above.

### Genus *Eurytides* Hübner
### Type-species: *Eurytides iphitas* Hübner

*Eurytides* Hübner [1821] p. 197.

Frons normal, antenna dorsally scaled; fore wing with upper and lower discocellular straight, in line, upper as long as lower, radials normal or, less frequently, $R_1$ or $R_1$ and $R_2$ anastomosing with Sc; in one species $R_1$ lost. Hind wing normal, tail present or absent. Male eighth tergite usually with a pseuduncus; ninth segment freely movable within eighth; uncus distinct, fused with socii except at tip, or in one species completely fused; valve with complete armature. Female bursa with horn-like signum.

This genus contains five species-groups, which I arrange in two subgenera and three sections.

### Subgenus *Protesilaus* Swainson
### Type-species: *Protesilaus leilus* Swainson

*Protesilaus* Swainson, 1833: 93.
*Cosmodesmus* Haase, 1892: 15. Type-species: *Papilio protesilaus* Linnaeus.

#### Section I

Clasper of male with distal rim hardly emarginated.

This section comprises two groups, differing widely in adult external appearance and, so far as known, in early stages, but hardly showing even specific differences in male genitalia.

*Marcellus*-group: adult non-mimetic, long-tailed, white, green or yellow striped with black; larva of *marcellus* smooth with narrow, transverse stripes on dorsum; pupa terete, anteriorly truncate; hosts Anonaceae. Ten species, from North, Central and South America and the West Indies.

*Lysithous* group: adult mimetic of Troidini or Heliconiinae, black with red, yellow or white spots, rarely tailed; larva either pale with dark transverse and longitudinal bands (Burmeister, 1879), or dark and tuberculate with pale spots (Moss, 1919), pupa with abdominal segments greatly swollen, head rounded, dorsal thoracic horn abrupt and forward-directed. Fifteen species, Central and South America.

#### Section II

Clasper of male with distal rim deeply emarginated, the dorsal and ventral angles forming falcate processes.

This section comprises only the closely knit *protesilaus* group, with several species, mostly South American. The life-history of one species has been described by d'Almeida (1924).

### Subgenus *Eurytides* Hübner

*Eurytides* Hübner [1821] pl. [92].

Clasper of male without a prominent, mesally-directed, finger-like process; outer margin of clasper double, consisting of two subparallel, serrated flanges.

This subgenus contains two species-groups, represented by *E. dolicaon* (Cramer) and *E. thyastes* (Drury), respectively. The *dolicaon* group differs from the *thyastes* group in having $R_1$ or $R_1$ and $R_2$ anastomosed with Sc. As the two groups are virtually identical in wing-pattern and genitalia, I do not regard this difference as warranting even sectional separation. The type-species of *Eurytides* is a member of the *dolicaon* group. No life-history information on the subgenus is available.

*Thyastes* group: hind wing beneath with red or tawny line (or row of spots) parallel to distal margin; $R_1$ of fore wing free. Six species; Central and South America.

*Dolicaon* group: hind wing beneath without red line; $R_1$ and sometimes $R_2$ of fore wing anastomosed with Sc.

### Genus *Protographium*, novum
### Type-species: *Papilio leosthenes* Doubleday

External structure as in *Eurytides*. Uncus of male long, gradually tapering, and simple; socii perhaps represented by free lateral lobes at its base.

This monotypic genus is separated by very slight characters from *Eurytides;* in facies, too, it resembles *E. marcellus* (Cramer). However, the structure of the genitalia, as well as the detailed resemblance of pattern and the occurrence in the same geographic region, all suggest a close relationship between *Protographium* and *Graphium*. This genus is evidently one of the relicts of which so many survive in Australia. The preservation of the uncus distinguishes it from all other normal kite-swallowtails of the Old World.

The larva is described and the pupa figured by Waterhouse (1932). The larva is smooth, with transverse stripes. It apparently lacks the thoracic spines of *Graphium*. The pupa lacks a dorsal horn, but is otherwise like that of *Graphium*. The food-plant is *Melodorum* (Lauraceae).

The single species is confined to Australia.

### Genus *Iphiclides* Hübner
### Type-species: *Papilio podalirius* Linnaeus

*Iphiclides* Hübner [1819] p. 82.
*Podalirius* Swainson, 1832-33: 252. Type-species: *Podalirius europaeus* Swainson, *nec* Latreille, 1802.

Wing-venation as in *Protographium;* $R_1$ free; facies typical. Red pigment of *I.podalirius* of type B, but that of *I. podalirinus* (Oberthür) of type A. Male with uncus aborted, valve lanceolate, with simple clasper. Larva smooth, with segmental red spots and oblique yellow bands, on Rosaceae. Pupa papilioniform, without continuous longitudinal ridges on abdomen.

Two species; Palaearctic.

### Genus *Graphium* Scopoli
### Type-species: *Papilio sarpedon* Linnaeus

Wings variable in shape; fore wing with $R_1$ always and $R_2$ occasionally anastomosed with Sc. External structure in other respects like that of *Eurytides*, *Protographium* and *Iphiclides*. Eighth tergite of male simple or with a blunt pseuduncus; ninth segment telescoping within eighth; uncus vestigial or wanting; socii represented by membranous lobes. Mature larva so far as known with one pair of small, thornlike, dorsolateral spines on each thoracic segment. Pupa various, normally with two pairs of abdominal carinae and a prominent thoracic horn.

This large genus contains all Old-World Leptocircini that have Sc and $R_1$ anastomosed. Although the group taken as a whole is a varied one, species that differ widely in facies are often closely similar in structure. The armature of the valve varies in detail and degree of complexity, but the extremes are connected by obvious intermediate stages; the superficial nature of the differences in valve-armature is confirmed by the fact that these differences are not supported by any other known character of either sex.

The most primitive forms are Indo-Australian, and include the *codrus* group (in which I include *cloanthus* and *sarpedon*, on the basis of their similarity to *codrus* and allies in valve-ornamentation), the *eurypylus* group, and *agamemnon*. In spite of its close external resemblance to *eurypylus* and allies, *agamemnon* differs from these species in having a simple and rounded clasper rather than a triangular and spine-bearing one. I have not had an opportunity to examine several of the scarcer species of the *eurypylus* group, some of which appear transitional to *agamemnon* in pattern,

and it may be that these will prove to bridge the gap in genitalic structure. In the *codrus* group several species have bifid tarsal claws, as do *Lamproptera curius* and *Dabasa*.

All these primitive groups of *Graphium* agree in having the thickened rim of the valve clothed with equally developed, short, rather coarse setae all around the dorsal, posterior and ventral margins, except in species such as *sarpedon* in which the overgrowth of the clasper obliterates the margin or part of it.

The *wallacei* group, which I have not examined structurally, shows definite resemblances to *agamemnon* in maculation. It is distinguished from *agamemnon* and the *eurypylus* group by having $R_2$ as well as $R_1$ anastomosed with Sc. Study of the genitalia will doubtless establish the true affinities of the *wallacei* group.

The next stage in development of the genus *Graphium* is that in which the marginal setae of the valve are somewhat thickened and are divided into two groups; a ventral or ventro-lateral one of variable extent and a dorsal one borne on a conspicuous and usually finger-like tubercle or process. All of the numerous African species of *Graphium*, and no others, belong to this stage of development.

Finally comes a third series in which one or both of the marginal seta-groups of the second series become dense patches of black spines. This specialized group is Indo-Australian, and includes the non-mimetic *antiphates* group and the mimetic *macareus* group. The two groups are not significantly different in genitalic structure. The four closely related species *eurous*, *mandarinus*, *alebion* and *tamerlanuy* Oberthür differ in having the patches of black setae replaced by serrated ridges, so that the valve superficially resembles that of *cloanthus* or *sarpedon*. The structure of the clasper shows that the true affinities of these forms are with such members of the *antiphates* group as *agetes* and *nomius*. The differences in genitalia and maculation seem sufficient to justify the separation of *eurous* and allies as a distinct species-group.

I recognize the three major divisions of *Graphium* as subgenera.

### Subgenus *Graphium* Scopoli
### Type-species: *Papilio sarpedon* Linnaeus

*Graphium* Scopoli, 1777: 433.
*Idaides* Hübner [1819] p. 85. Type-species: *Papilio codrus* Cramer.
*Zetides* Hübner [1819] p. 85. Type-species: *Papilio sarpedon* Linnaeus.
*Chlorisses* Swainson, 1832-33: 89. Type-species: *Papilio sarpedon* Linnaeus.
*Semicaudati* Koch, 1860: 231. Type-species: *Papilio sarpedon* Linnaeus.
*Dalchina* Moore, 1881: 143. Type-species: *Papilio sarpedon* Linnaeus.
*Zethes* Swinhoe, 1885: 145. Type-species: *Papilio agamemnon* Linnaeus.

Rim of male valve without a dorsal setiferous or spiniferous tubercle. Tail of hind wing short and blunt, or absent. In the *wallacei* group $R_2$ anastomosed with Sc, in other groups $R_2$ free.

*Codrus* group: species with an expanded, distally serrate, male clasper, viz.: *macleayanus* (Leach), *weiskei* (Ribbe), *codrus* (Cramer), *empedocles* (Fabricius), *cloanthus* (Westwood), and *sarpedon*.

*Eurypylus* group: species with clasper short, triangular, and armed with a few prominent thorn-like spines; *doson* (Felder), *evemon* (Boisduval), *eurypylus* (Linnaeus), ? *procles* (Grose-Smith), ? *meyeri* (Hopffer), *bathycles* (Zincken), *leechi* (Rothschild), ? *macfarlanei* (Butler), *mendana* (Godman and Salvin), *arycles* (Boisduval).

*Agamemnon* group: species with clasper short and rounded; *agamemnon* (Linnaeus), ? *meeki* (Rothschild).

*Wallacei* group: genitalia not studied; maculation similar to that of *agamemnon* group, but $R_2$ as well as $R_1$ anastomosed with Sc. Species: *wallacei* (Hewitson), *browni* (Godman and Salvin), *hicateon* (Math.).

**Subgenus *Arisbe* Hübner**

**Type-species: *Papilo similis* Cramer**

*Zelima* Fabricius, 1807: 279. Type-species: *Papilio pylades* Fabricius, *nec* *Zelima* Meigen, 1800 [Diptera].

*Arisbe* Hübner [1819] p. 89.

*Ailus* Billberg, 1820: 81. New name for *Zelima* Fabricius, and consequently isogenerotypic therewith.

An application for the suppression of the Meigen 1800 names is now before the International Commission on Zoological Nomenclature. My colleague Dr. J. R. Vockeroth tells me that to the best of his knowledge the name *Zelima* Meigen, 1800, was not again used between the time of original description and 1807. Therefore if *Zelima* Meigen, 1800, is suppressed, *Zelima* Fabricius, 1807, will become a valid name, and will supplant *Arisbe* Hübner [1819].

Rim of male valve with stout setae concentrated on disto-ventral half and on a dorsal process, but the setae not modified into spines in either region.

The species-groups of this subgenus have been excellently classified by Berger (1951). Because his study was confined to the Ethiopian fauna Berger was led to emphasize the differences rather than the resemblances between the species: the fundamental homogeneity of the African forms becomes apparent only after comparison with the Oriental and the American groups of the tribe.

Larvae of some species have been figured by van Son (1949) from original paintings by Gowan C. Clark. Van Son gives also excellent figures of male and female genitalia of the southern African species.

I have no reason to change Berger's arrangement of species-groups.

*Antheus* group: hind wing tailed; valve with low dorsal tubercle, distal margin armed with four to six strong teeth; clasper tridentate and occupying whole inner face of valve. Two species: Africa and Madagascar.

*Porthaon* group: hind wing tailed; valve with long dorsal process, as in all following groups, and with posteroventral angle produced into a distally swollen and denticulate process. One species: South and East Africa.

*Colonna* group: hind wing tailed; clasper broad, without ventral process, but with two simple dorsal processes extending beyond costa of valve. One species: South and East Africa.

*Policenes* group: hind wing tailed; clasper with long dorsal process, extending well past dorsal margin of valve, and ending in two dentate flanges perpendicular to each other; dorsal process of valve flattened. About five species: African mainland.

*Illyris* group: hind wing tailed; pale markings restricted; male genitalia small; dorsal process of clasper narrow, extending beyond dorsal margin of valve; ventral process slender, strongly denticulate posteriorly. Three species: East and West Africa; Fernando Po.

*Philonoë* group: male genitalia small and weakly sclerotized; dorsal process of clasper very long, broadened and weakly denticulated at tip; ventral process straight, not denticulate. One species: East Africa.

*Leonidas* group: wings tailless and with danaid-like maculation; male genitalia robust; dorsal process of clasper short, wide, and distally dentate; ventral process dentate distally. Three species: Africa, Madagascar and Comoros.

*Ucalegon* group: wings tailless; pattern mimetic; dorsal process of clasper simple, bent, ending in a point; dorsal process of valve slender, cylindrical, and pointed. Twelve species: Central and West Africa.

*Tyndaraeus* group: wings tailless; pattern complex; dorsal process of clasper bifid, ventral process ending in forceps-like points. Two species: Central and West Africa.

*Pylades* group: wings tailless, pattern irregular; clasper with a sub-basal lamella, absent in other groups.

### Subgenus *Pathysa* Reakirt
### Type-species: *Papilio antiphates* Cramer

*Pathysa* Reakirt, 1864: 503.
*Paranticopsis* Wood-Mason and de Nicéville, 1887: 376. Type-species: *Papilio macareus* Godart.
*Pazala* Moore, 1888: 283. Type-species: *Papilio glycerion* G. R. Gray.
*Deoris* Moore, 1903: 31. Type-species: *Papilio agetes* Westwood.

Generally similar to the subgenus *Arisbe*, and evidently derived from it; differing in having at least the setae of the dorsal process of the valve, and usually those of the ventral margin too, developed into stout, black, easily dislodged spines, or, alternatively, replaced by prominent serrated ridges.

I recognize three species-groups, mainly following Jordan (1908-09). As I have studied less than half the species, some rearrangement may ultimately be needed in the *antiphates* and *macareus* groups.

*Antiphates* group: dorsal process of valve armed with spines, ventral margin with spines or stout setae. Long-tailed, non-mimetic species. This is the *antiphates* group of Jordan (1908-09) less *leosthenes*, *podalirius*, *eurous*, *mandarinus*, and *alebion*, which I have placed elsewhere.

*Macareus* group: genitalia as in the *antiphates* group. Mimetic species, normally tailless, but one species (*phidias* Oberthür) with a tail.

*Eurous* group: valve with two dorsal and one ventral serrate ridges, in addition to the ridged and serrate clasper. Dorsal process and articulated marginal spines and setae lacking. Four species: *eurous* Leech, *mandarinus* Oberthür (*glycerion* Gray, *nec* Borkhausen), *alebion* Gray, and *Tamerlanus* Oberthür. It would not be unreasonable to separate this group as a fourth subgenus, for which the name *Pazala* is available, but the affinities of the group are plainly here and I prefer not to multiply subgenera unnecessarily.

### Genus *Dabasa* Moore
### Type-species: *Papilio gyas* Westwood

*Dabasa* Moore, 1887: 283.
*Meandrusa* Moore, 1887: 284. Type-species: *Papilio evan* Doubleday.

$R_1$ and $R_2$ free from Sc. Fore wing and udc short, mdc long and outwardly concave, discal cell broad. Tarsal claws toothed. Male eighth abdominal tergite prolonged into a slender false uncus like that of *Papilio*; ninth tergite medially weakened, joined to base of false uncus; socii strongly sclerotized, apposed, shoe-shaped; valve rounded; clasper short, triangular; aedoeagus fairly stout; juxta with strong lateral flaps. Wings with red pigments and anthoxanthins lacking.

The strong cleavage between this genus and the other Leptocircini seems not to have been generally noticed. The short upper discocellular is reminiscent of *Teinopalpus* and other primitive forms. There are only two species, not particularly closely related. Unfortunately the early stages are unknown. Range: Oriental.

### Tribe Papilionini

Antenna scaleless, with sense-hairs of under surface in a diffuse patch on each segment, not sunk in pits. Tarsi with dorsal spines separated from ventral ones by a spineless, impressed space. Wings broad; cell of fore wing large; upper and middle discocellular usually not in line; 2nd and 3rd A free or stalked; anal region of hind wing not sexually modified. Male with eighth abdominal tergite normally prolonged into a posterior, uncus-like process, the process dorsally scaled; ninth and tenth segments membranous mid-dorsally, ninth tergite firmly attached to eighth, socii well developed, strongly sclerotized, always depressed at an angle to the false uncus, sometimes with coarse setae as in Troidini; valve large and usually elongate, clasper usually conspicuous and toothed or serrate; juxta of moderate size, usually heart-shaped or V-shaped.

Female with prominent ostial armature, consisting typically of a large anterior and a smaller posterior plate or boss, and a pair of lateral plates, but often greatly elaborated by the development of flanges and teeth; bursa membranous, with a long, strap-like, medially seamed, ventral signum.

Larva when young bearing rows of spiny tubercles, typically dark with red or pale spots and a pale saddle on abdominal segments 3 and 4. Older larva sometimes retaining the juvenile facies, more often with spines lost except for rudiments on first and last segments, and with pattern variously modified. Pupa with two anterior processes on head, a pair of lateral processes and a dorsal process on thorax, and obscure, paired, dorso-lateral and lateral rows of tubercles or carinae on abdomen; texture rough or smooth; long axis of pupa straight, or simply or sigmoidally bent.

Food-plants mainly Lauraceae and Rutaceae, but a number of species of Rutaceae-feeding groups transferring partly or wholly to Umbelliferae; a few species with other food plants. No species known on Aristolochiaceae, Combretaceae, or Anonaceae.

The superficial diversity of this tribe has led to many attempts to divide it generically. Unfortunately there is an almost complete lack of structural differences suitable for characterizing generic divisions. Wing-venation and the structure of legs, palpi, and antennae are constant except in minor details; the few differences are subtle in nature and erratic in distribution, extremes of variation often being reached in closely related species. Both male and female genitalia are very uniform in basic structure. The male shows nothing like the striking modifications seen in the Leptocircini or the Troidini. The structure of the valve varies widely, but without particular system, sometimes differing greatly in closely allied species (*menestheus* group, *nireus* group), at other times varying little in extended and varied series of species (Subsection A of Section II.). The female signum is of one type throughout the tribe; the periostial armature varies, but again some of the largest differences are between closely related species (*machaon* group, *glaucus* group.)

Pattern is of considerable help in determining relationship, but here as in other groups it is far too erratic to be used to define genera. Distantly related species may show misleading resemblances (*alexanor* and *glaucus; demoleus*, *demolion*, and *thoas*), whereas closely related groups and species or even forms or sexes of single species may be totally dissimilar in appearance.

The detailed structure of the larvae has so far not been studied. An interesting field of investigation lies open here. However, even the maculation and gross anatomy yield interesting evidence on relationships. The young larvae of all species that have been studied are dark in colour with rows of low, setose or spiny tubercles. There is almost always a pale V-shaped patch or "saddle" on the third and fourth abdominal segments, and there are often lateral pale patches on the thorax and on the posterior part of the abdomen.

The mature larvae are much more varied. In a large series of Asiatic forms the pale patches of the young larva become expanded and green in the last instar; the upper surface is in that stage predominantly green, divided only by narrow brown bands, particularly a tapering one on the first abdominal segment, an oblique one on abdominal segments 4 and 5 (representing the posterior edge of the primitive "saddle") and another tapering one on the posterior part of abdominal segment 6.

Some species of this Asiatic complex preserve spiny tubercles in the last instar. In the *aegeus* group a complete set of paired dorsal spines is retained, supplemented by subdorsal and lateral spines on the meso- and meta-thorax; these tubercles are concolorous with the bands or fields on which they stand. In the *godeffroyi* group the tubercles are contrastingly red, and are lacking on the middle or the middle and posterior abdominal segments. In the closely related *fuscus* and *polytes* groups the red tubercles are lost. In the *demolion* group dorsal tubercles are retained on one or more of the brown abdominal bands but are absent elsewhere. In *P. woodfordi*, in the gloss-Papilios

and in at least some African groups the tubercles of the prothorax and of the ninth abdominal segment are fairly well preserved, but others are lacking. In the *fuscus*, *memnon* and *helenus* groups these tubercles are weaker or suppressed. The fate in the various groups of the row of tubercles on the metathorax is interesting. In the *demolion* and *polytes* groups this row is replaced by a brown band, either plain or ornamented. In the *memnon* and *helenus* groups and in such African species as *nireus*, the lateral extremities of the band are developed into more or less distinct eye-spots. In the gloss-papilios and in the African *P. dardanus* these eye-spots stand alone.

The *demoleus* group has varied larvae. The larva of *P. demoleus demoleus* has a simple brown band on the metathorax and is rather *polytes*-like. The typical larva of *P. demodocus* is *memnon*-like, with a raised metathoracic band ending on each side in an eye-spot. The larva of the Australian *P. demoleus sthenelus* Macleay is described as being quite distinct; it is said to be green, with paired dorsal and sub-dorsal rows of yellow spots. The Umbelliferae-feeding form of *P. demodocus*, described by van Son (1949) is even more remarkable, being white, with longitudinal black bands and segmental spots, and with segmental orange-red spots. *P. xuthus* Linnaeus has a green, eye-spotted larva with segmental orange spots. I think there is little doubt that the relationships of the *machaon* group, with its black-banded and orange-spotted umbellifer-feeding larvae, are to *demoleus* and *xuthus;* the spiny larva of the otherwise specialized *P. hospiton* is doubtless atavistic. *P. anactus* Macleay connects this group to the *laglaizei* group, which has a closely similar larva.

All the groups so far discussed are confined to the Old World and either feed on Rutaceae, or can plausibly be derived from Rutaceae-feeders. In the New World there are two sections of *Papilio* with green, eye-spotted larvae. These differ from the Old-World groups with similar larvae in that one so far as known feeds exclusively on Lauraceae and immediate allies, and the other appears to have fed primitively on these same groups, though some of the species now feed rather generally on deciduous trees and shrubs. The tropical-American *homerus* and *scamander* groups have smooth, green, eye-spotted larvae with an X-shaped "saddle". The known species feed on Lauraceae and the closely related Hernandiaceae. The North-American *glaucus* and *troilus* groups have smooth, green, eye-spotted larvae which, according to Forbes' theory, fed primitively on Lauraceae and Magnoliaceae. These larvae have, according to Forbes, an extra row of proleg crochets, a primitive feature lost in most of the few species of Papilionidae that have been examined for this character.

There are Lauraceae-feeding larvae in the Old World too, but there they are of a very different type. In the Lauraceae-feeding *clytia* and *agestor* groups the larva is fuscous with black tubercles, segmental red spots and large white or yellowish side-patches. These pattern-elements are similar to those of young larvae of the Old-World citrus-feeding group. It may be that *clytia* and its allies are primitive, as the lauraceous food-plant would suggest, or it may be that the larvae are regressive, the juvenile type perhaps having been favoured by a resemblance to troidine larvae. In the latter event the close resemblance of the adults to those of the *castor* group may be taken as evidence of relationship, but if the *clytia* group is primitive the resemblance must be considered convergent.

Conversely, there is in the New World a considerable assemblage of Rutaceae-feeding Papilionini. The larvae of these are mottled brown, with large whitish lateral patches disposed in the typical young-larva pattern. The three groups with this kind of larva form a closely knit section. There are two subordinate types of larvae: that found in the *thoas* group, which when mature is unspined and solitary; and that of the *torquatus* and *anchisiades* groups, which even when mature is armed with short spiny tubercles, and which is usually gregarious, resting on tree-trunks when not feeding. Although the larvae of this group look very different from those of the Old-World Rutaceae-feeding groups, having a brown, bark-matching instead of a green, leaf-

matching pattern, they are basically similar to those of the *helenus* group in pattern and structure.

The pupae show less striking and consistent characters than the larvae, the genus as a whole having a general uniformity of structure, with as usual an erratic distribution of superficial differences. In general the pupae may be rough (*cresphontes*, *memnon*) moderately smooth (*troilus*) or very smooth (gloss-papilios, *dardanus*); they may be straight (*glaucus*, *clytia*) slightly bent (*machaon*) moderately bent (*troilus*, *cresphontes*, *ulysses*) strongly bent (*bridgei*, *polymnestor*, *euchenor*) or very strongly bent (*demolion*). There is variation in the processes: blunt, anteriorly directed processes give a stick-like appearance in *clytia* and *agestor;* there is a long dorsal process in *demolion;* there are long anterior processes in *polytes*. The pupa may be almost cylindrical (*clytia*, *agestor*) or much depressed (*dardanus*), with all intermediates.

As already indicated, I have failed to find simple and reliable differentiating characters for what appear to be the natural groups of Papilionini. I therefore include all the species in a single genus.

## Genus *Papilio* Linnaeus
### Type-species: *Papilio machaon* Linnaeus

*Papilio* Linnaeus, 1758: 448.
*Pterourus* Scopoli, 1777: 433. Type-species: *Papilio troilus* Linnaeus.
*Princeps* Hübner [1807] pl. 116. Type-species: *Princeps demoleas* Hübner.
*Amaryssus* Dalman, 1816: 60. Type-species: *Papilio machaon* Linnaeus.
*Jasoniades* Hübner [1819] p. 83. Type-species: *Papilio turnus* Linnaeus.
*Euphoeades* Hübner [1819] p. 83. Type-species: *Papilio glaucus* Linnaeus.
*Heraclides* Hübner [1819] p. 83. Type-species: *Papilio thoas* Linnaeus.
*Menelaides* Hübner [1819] p. 84. Type-species: *Papilio polytes* Linnaeus.
*Achillides* Hübner [1819] p. 85. Type-species: *Papilio paris* Linnaeus.
*Orpheides* Hübner [1819] p. 86. Type-species: *Papilio demoleus* Linnaeus, 1764 *nec* 1758.
*Nestorides* Hübner [1819] p. 86. Type-species: *Papilio gambrisius* Cramer.
*Calaides* Hübner [1819] p. 86. Type-species: *Papilio androgeus* Cramer.
*Priamides* Hübner [1819] p. 87. Type-species: *Priamides hipponous* Hübner.
*Iliades* Hübner [1819] p. 88. Type-species: *Papilio memnon* Hübner.
*Troilides* Hübner [1825] pl. 324. Type-species: *Troilides tros* Hübner.
*Clytia* Swainson, 1833: 120. Type-species: *Papilio clytia* Linnaeus.
*Thoas* Swainson, 1833: 148. Type-species: *Papilio thoas* Linnaeus.
*Aërnauta* Berge, 1842: 19. Type-species: *Papilio machaon* Linnaeus.
*Ecaudati* Koch, 1860: 230. Type-species: *Papilio memnon* Linnaeus.
*Caudati* Koch, 1860: 230. Type-species: *Papilio turnus* Linnaeus.
*Pyrrhosticta* Butler, 1872: 86. Type-species: *Papilio laetitia* Butler.
*Druryia* Aurivillius, 1881: 44. Type-species: *Papilio antimachus* Drury.
*Harimala* Moore, 1881: 145. Type-species: *Papilio crino* Fabricius.
*Charus* Moore, 1881: 149. Type-species: *Papilio helenus* Linnaeus.
*Chilasa* Moore, 1881: 153. Type-species: *Papilio dissimilis* Linnaeus.
*Sarbaria* Moore, 1882: 258. Type-species: *Papilio polyctor* Boisduval.
*Cadugoides* Moore, 1882: 258. Type-species: *Papilio agestor* G. R. Gray.
*Sainia* Moore, 1882: 260. Type-species: *Papilio protenor* Cramer.
*Araminta* Moore, 1886: 50. Type-species: *Papilio demolion* Cramer.
*Pangeranopsis* Wood-Mason and de Nicéville, 1887: 374. Type-species: *Papilio elphenor* Doubleday.
*Panosmiopsis* Wood-Mason and de Nicéville, 1887: 379. Type-species: *Papilio rhetenor* Westwood.
*Euploeopsis* de Nicéville, 1887: 433. Type-species: *Papilio telearchus* Hewitson.
*Menamopsis* de Nicéville, 1887: 433. Type-species: *Papilio tavoyanus* Butler.
*Isamiopsis* Moore, 1888: 284. Type-species: *Papilio telearchus* Hewitson.
*Tamera* Moore, 1888: 284. Type-species: *Papilio castor* Westwood.
*Achivus* Kirby, 1896: 286. Type-species: *Papilio machaon* Linnaeus.
*Eques* Kirby, 1896: 290. Type-species: *Papilio nireus* Linnaeus.
*Icarus* Röber, 1898: 185. Type-species: *Papilio zalmoxis* Hewitson.[4]

[4]"*Iterus*" "Süffert" or "Dönitz", given as a genus by Bryk (1930) and by Neave (1939), is evidently an erroneous subsequent spelling of *Icarus* Röber.

*Melindopsis* Aurivillius, 1898: 461. Type-species: *Papilio rex* Oberthür.
*Sadengia* Moore, 1902: 213. Type-species: *Papilio nephelus* Boisduval.
*Mimbyasa* Evans, 1911: 972. Type-species: *Papilio janaka* Moore.
*Agehana* Matsumura, 1936: 86. Type-species: *Papilio elwesi* Leech.

I divide the genus *Papilio* into five sections. Because these sections cannot be defined by any simple system of adult characters, and as they are all nearly related, I do not dignify them as subgenera, though names are available in abundance.

**Section I**

Adults mimetic of Danainae or Euploeinae; male clasper broad and serrate. Larva dark, with conspicuous pale bands or patches, spiny tubercles, and orange segmental spots; so far as known feeding on Lauraceae. Pupa so far as known cylindrical and stick-like, or *machaon*-like.

Further study may show that this section should be united with the following one.

*Agestor* group: Sc of hind wing arising from cell distad of $Cu_2$; larva with large white lateral patches, on Lauraceae. Three species, Nepal and West China to Sumatra and Borneo.

*Clytia* group: Sc of hind wing arising closer to base than $Cu_2$; larva as in preceding group. Two species, China and Himalayas to Java and Palawan.

*Veiovis* group: Dr. Wm. T. M. Forbes has pointed out to me that the single species of this group is distinguishable from the members of *clytia* group by two important peculiarities: (1) the vestigial media in the cell of the fore wing is forked much further out than is usual in *Papilio* (Moore shows a similar structure in one of the specimens of *P. epycides* Hewitson, *agestor* group, that he figures); and (2) the submarginal spots of the hind wing are divided in the middle of each cell, as is usual in African species of *Papilio*. The valve of *P. veiovis* Hewitson has a broad clasper with prominent teeth. The life history is unknown. Range: Celebes.

*Laglaizei* group: adult mimetic of Uraniidae; larva with orange segmental bands and yellow spots or black with orange tubercles; food-plant unknown. Three species, Papuan Region.

**Section II**

Adult extremely varied. Larva usually green with transverse band on first abdominal segment and an oblique band on fourth and fifth segments; often with an additional transverse band on sixth abdominal segment. Tubercles present or absent.

The larvae are described in more detail in the general discussion of the tribe, above. They feed primarily on Rutaceae, less commonly on Umbelliferae and other derivative hosts.

This very large section includes all the remaining Old-World groups of the genus. I distinguish two subsections: one comprises the Oriental species, together with *menestheus* and allies and *demodocus* and allies from the Ethiopian Region; the other comprises the remaining Ethiopian species. The African subsection is much less homogeneous than the Oriental one — an interesting contrast to the condition in the Leptocircini. When we have better knowledge of genitalia and life-histories the African subsection may have to be subdivided.

**Subsection A**

Clasper of male valve almost invariably consisting of a slender ventral rod dilated distally into a narrow, marginally denticulated plate. The uniformity of male genitalia in this superficially diverse subsection is very striking. Only the *demolion* and *ulysses* groups have significantly different valve-armature, and these are linked to more normal species by other characters. There are two fairly distinct series: the non-metallic forms and the metallic "gloss-papilios." The larvae of the former may have

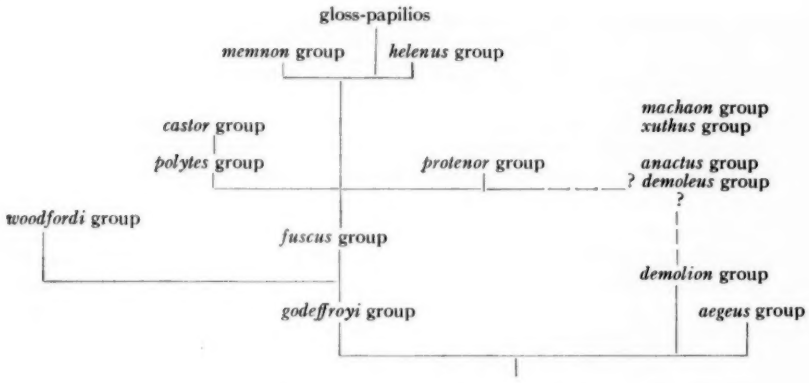


Fig. 2. Apparent phylogeny of groups of Subsection A, Section II of *Papilio*.

a ridge on the first abdominal segment, but they do not have the dorsal surface of the thorax and first abdominal segment developed into an oval, shield-like, raised area such as is found in gloss-papilio larvae. In the first series the pupa is rough, whereas in the gloss-papilios it is smooth and has the cephalic and thoracic processes reduced. The apparent relationships of the groups are shown in Fig. 2.

**Series 1**

*Aegeus* group: adult tailless, with conspicuous black-and-white pattern; larva with complete series of tubercles, concolorous with ground; hosts Rutaceae. Species: *aegeus* Donovan and *bridgei* Mathew; and presumably also *tydeus* Felder, *gambrisius* Cramer, *inopinatus* Butler, and *oberon* Grose-Smith, but the larvae of these four are unknown. Range: Papuan.

*Godeffroyi* group: adult black and white, tailed; larva with red tubercles anteriorly and sometimes posteriorly; hosts Araliaceae. Species: *godeffroyi* Semper, *schmeltzi* Herrich-Schäffer, and probably *amynthor* Boisduval (*ilioneus* Don. *nec* A. and S.) Range: Pacific Islands.

*Woodfordi* group: adult tailless, black and white, as in *aegeus* group; larva lacking saddle and metathoracic band, with band of first abdominal segment narrow, oblique and raised, and with a pair of dorsal tubercles on prothorax and another on ninth abdominal segment; hosts Rutaceae. Species: *woodfordi* Godman and Salvin, and probably *ptolychus* Godman and Salvin and *erskinei* Matthew. Range: Solomon Islands.

*Fuscus* group: adult tailed, black with more or less well-defined white postmedial band, somewhat expanded in costal half of hind wing. Larva smooth, green variegated with brown, without tubercles or eye-spots; hosts Rutaceae. Species: *fuscus* Goeze and *canopus* Westwood, and possibly *diophantus* Grose-Smith, *antonio* Hewitson, *noblei* de Nicéville, *albinus* Wallace, *hipponous* Felder, *sakontala* Hewitson, *jordani* Fruhstorfer and *walkeri* Janson. Range: Indo-Australian.

*Castor* group: sexually dimorphic, males like those of following groups, but always tailless, females mimetic of Danainae; abdomen in both sexes with segmental rows of white dots; genitalia and larva much as in *fuscus* and *polytes* groups; hosts Rutaceae. Three species: India to Formosa and Malaya.

*Polytes* group: sexually dimorphic, or with polymorphic females, in part mimetic of Troidini; larva green with the usual transverse band somewhat ornate but without

eye-spots; hosts Rutaceae; range Indo-Australian. Species: *polytes* Linnaeus, *ambrax* Boisduval, *phestus* Guérin.

*Helenus* group: adult as in *fuscus* group, but with submarginal band obsolescent except for the large white patch occupying three or four cells on anterior half of hind wing; larva with bands of metathorax and first abdominal segment raised, the metathoracic band ending in a prominent eye-spot; hosts Rutaceae. Species: *helenus* Linnaeus, *sataspes* Felder, *iswara* White, *iswaroides* Fruhstorfer, *chaon* Westwood, *nubilus* Staudinger, and *nephelus* Boisduval. The larvae of most of the species remain to be described, and it will not be surprising if the group proves to intergrade with the *fuscus* group. Range: Ceylon and Japan to Celebes and Timor.

*Memnon* group: Males tailless, females often polymorphic, with some forms tailed, in part mimetic of Troidini; larva exactly as in *helenus* group; hosts Rutaceae. Species: *ascalaphus* Boisduval, *oenomanus* Godart, *polymnestor* Cramer, *lampsacus* Boisduval, *forbesi* Grose-Smith, *acheron* Grose-Smith, *mayo* Atkinson, *lowi* Druce, *memnon* Linnaeus, *rumanzovia* Eschscholtz and *deiphobus* Linnaeus. The last two species are the only members of the genus that have red pigment A, but they are otherwise unremarkable. Range: Japan and India to Waigeu.

*Protenor* group: tailless or tailed, mimicking Troidini; larva without eye-spots, resembling that of *polytes* group; hosts Rutaceae. Species: *protenor* Cramer, and probably *demetrius* Cramer, *alcmenor* Felder, and *thaiwanus* Rothschild. Range: Himalaya to Burma and Japan.

*Bootes* group: tailed, mimicking Troidini; head and a lateral abdominal band red; early stages unknown. Species: *janaka* Moore, *bootes* Westwood, and *elwesi* Leech. Range: Himalayas and China.

*Demolion* group: adult with blue eye-spots at anal and apical angles of hind wing beneath; normally tailed and with transverse yellow bands on wings, but one species (*euchenor*) tailless and black-and-white like *aegeus;* clasper broad and bidentate (*demolion, euchenor*), or normal (African species); larva with a pair of tubercles on prothorax, on abdominal segments 5 and 9, and sometimes on segment 6; pupa in Asiatic species reflexed and sometimes armed with a long thoracic horn, but in *euchenor* and the African *ophidicephalus* with a normal horn, and in *ophidicephalus* not reflexed; hosts Rutaceae. Range: Ethiopian, Oriental, and Papuan regions, the African and Indo-Australian forms comprising distinct subgroups. Species: *demolion* Cramer, *liomedon* Moore, *gigon* Felder, and *euchenor* Guérin (Subgroup a); *menestheus* Drury, *lormieri* Distant, and *ophidicephalus* Oberthür (Subgroup b).

*Demoleus* group: pattern as in the last group, but with the bands of yellow spots irregular; tail absent or nearly so; larvae *polytes*-like, *memnon*-like, or with regular pattern of black and reddish spots or bands. Hosts: Rutaceae, Umbelliferae and rarely other plants. Species: *demoleus* Linnaeus, *demodocus* Esper, *erithonioides* Grose-Smith, *morondavana* Grose-Smith, *grosesmithi* Rothschild. Range: Ethiopian, Malgassic, Oriental, and Papuan regions.

*Xuthus* group: adult similar in external appearance to those of following group, but with genitalia like those of preceding groups; larva green with eye-spots and red segmental spots; hosts: Rutaceae. The single species occurs in the eastern Palaearctic region.

*Machaon* group: adult black, or yellow banded with black, hind wing with a median band in one species; larva in most species smooth and green with segmental black bands and yellow or orange spots; in *hospiton* the larva with segmental spines and a complex dark pattern. Hosts: mainly Umbelliferae, but also Rutaceae, Compositae etc. Species: *alexanor* Esper, *hospiton* Guenée, *machaon* Linnaeus, *oregonia* Edwards, *zelicaon* Lucas, *polyxenes* Fabricius, *brevicauda* Saunders, *indra* Reakirt, etc. Precise species limits in this group are currently under experimental investigation by Remington and others. Range: Holarctic to Central America.

### Series 2

#### Gloss-papilios

*Paris* group: pattern similar to that of *helenus* and *fuscus* groups, but with pale areas replaced by brilliant metallic blue or green; larva with shield-like dorso-anterior thickening and with small metathoracic eye-spots; pupa smooth and green; hosts Rutaceae. Nine species. Range: Himalayas and Japan to Java and Borneo.

*Palinurus* group: upperside of wings with a broad blue or green metallic band; early stages as in *paris* group. Four species. Range: India and Ceylon to Celebes.

*Peranthus* group: basal part of wings above broadly metallic green or blue; colour-sequence in submarginal spots of under side of hind wing yellow-black-blue; early stages unknown. Four species. Range: Java to New Guinea.

*Ulysses* group: basal part of wings above broadly metallic blue; colour-sequence in submarginal spots of under side of hind wing blue-yellow-black; larva not unlike that of *woodfordi*, green, with white lateral line and raised white band on first abdominal segment, long pale tubercles on ninth abdominal segment, and large white dorso-lateral patches on abdominal segments 3 to 8; pupa smooth and green with no dorsal horn, but with sharp cephalic one; food-plants Rutaceae. A relationship between this group and the Jamaican *P. homerus* (Section V) has been suggested to me, but the larvae, pupae, food-plant, genitalia, and sex-scaling are all different, and indeed the differences in general facies are probably more striking than the resemblances. The genitalia of *P. ulysses* Linnaeus differ widely from those of the preceding groups, having a broad bicornuate clasper and stout, distally serrate socii. Jordan (1908-9) says that the genitalia of *P. montrouzieri* Boisduval are very different, but he does not describe them. Two species. Range: Papuan.

#### Subsection B

This subsection comprises all the purely African groups. The species are just as diverse in external appearance as those of Subsection A, and are much more varied in genitalic structure. Such closely allied species as *P. bromius* and *P. nireus* have strikingly different claspers, and, although some of the groups are more homogeneous than the *nireus*-group, there are wide differences between different groups. The larvae are obviously similar to those of Subsection A, and like them feed on Rutaceae. They are not, however, clearly linked with any particular group in the Asiatic subsection, and indeed the larvae of different species show resemblances to different Asiatic species: *P. nireus* has a somewhat *memnon*-like larva, with a raised metathoracic band ending in a pair of eye-spots; *P. dardanus* has reduced eye-spots like those of the *paris* group; and *P. echerioides* lacks any trace of the metathoracic band. The smooth pupa and shield-like larval notum of *dardanus* and *nireus* suggest a relationship to the gloss-papilios, but the pupa of *echerioides* is rough and laterally flanged (see figure by Gowan C. Clark, in van Son, 1949).

The main character uniting these African groups is the strong tendency for the submarginal lunule of each cell to be divided along the central fold. This tendency is particularly strong on the hind wing, but is manifested also on the fore wing in many species. At least some species in every African group show this characteristic, which is extremely rare in non-African papilios, occurring to my knowledge only in *veiovis* and *slateri* Hewitson of Section I. This character, originally pointed out to me by Dr. Forbes, must, I think, be given considerable weight, particularly when the great diversity in general appearance of the African insects is considered.

The classification given by Berger (1951) is I believe nearly as good as can be drawn up with present knowledge. Berger has examined the male genitalia of all known African species. Some changes will probably have to be made in his system with increasing knowledge of early stages and after study of the female genitalia, but I think its main outlines will prove to be in most respects sound. I adopt it almost

without change, except for the removal of *leucotaenia* from the *menestheus* group, which I have united above with the *demolion* group and which I have referred, together with the *demoleus* group, to Subsection A. As Berger has characterized the groups and listed the species, I content myself with a brief synopsis.

*Nireus* group: dark species with lustrous bands, usually green or blue-green, on the upper side of the disc; tailed or tailless; male with false uncus straight, unusually deep and compressed; clasper dentate, lying along mid-axis of valve. Berger distinguishes the following four subgroups. *mackinnoni* subgroup, three species; *sosia*-subgroup, one species; *bromius* subgroup, five species; *nireus* subgroup, three subspecies. Some rearrangement of these subgroups may ultimately be needed. I suspect that *oribazus* Boisduval, *epiphorbas* Boisduval, and *phorbanta* Linnaeus may be closely related to one another and that they may have some connection with *charopus* Westwood and *hornimani* Distant; *sosia* R. and J., *brontes* Godman, *bromius* Doubleday, and *nireus* Linnaeus have the appearance of being another closely connected group. The early stages of *bromius* are like those of *nireus*, already discussed under the subsection heading.

*Zalmoxis* group: the straight, compressed false uncus is reminiscent of that of the preceding group; the blue colour of the wings is unique; Le Cerf has suggested that the genitalia resemble those of Troidini, but the similarity is purely superficial, as is immediately evident when a large number of troidine species are examined. Life-history unknown. One species.

*Antimachus* group: wings elongate, pattern *Acraea*-like; uncus weakly hooked, but strongly compressed as in the preceding groups; clasper long, tapering, serrated, in middle of valve; eighth tergite of male with a pair of lateral thorns as in the *gallienus* group. One species. Life-history unknown.

*Rex* group: danaid-mimics in both sexes; male with androconial patches on internervular folds of fore wing. One species. Life-history unknown.

*Cynorta* group: males tailless, females mimetic of *Amauris* or of *Bematistes;* genitalia not unlike those of the typical subgroup of the *phorcas* group; female genitalia (*echerioides* Trimen, *cynorta* Fabricius, and *zoroastres homeyeri* Plötz) somewhat like those of *P. dardanus*, but unlike those of *constantinus* Ward, *euphranor* Trimen, and *hesperus* Westwood. Larva and pupa (*echerioides*) widely different from those of *dardanus*. Seven species.

*Phorcas* group: clasper narrow, fused for a considerable distance with ventral margin of valve. Berger recognizes two subgroups, the *dardanus* subgroup (five species) with ovate valve and the *hesperus* group (three species), with subquadrate valve. There would be some advantage in separating *P. dardanus* Brown, whose remarkable habitus and polymorphism, as well as its distally flanged clasper, are distinctive; *P. phorcas* Cramer and allies would then constitute a third subgroup. The *hesperus* subgroup is perhaps more nearly related to the *nireus* group than appears in this classification. Life-histories are badly needed in this group, as the only one known is that of *dardanus*.

*Delalandei* group: facies closely similar to that of tailed members of the *nireus* group; male with valve narrowed dorsally and with a blade-like, partly denticulate clasper fused with valve along ventral margin; aedoeagus strongly bent. Two species; Madagascar. I have not studied specimens of this or the next group.

*Leucotaenia* group: the single remarkable species is classed by Berger as a monotypic subgroup of his *menestheus* group; the general facies is, however, very different, and as the submarginal spots of the under side of the hind wing are divided I place this species in Subsection B. The genitalia are described as being like those of the last group, but with part of the clasper free. Range: Central Africa.

*Gallienus* group: with facies much as in *cynorta* group, but correctly separated by Berger on the basis of the different genitalia; false uncus strongly decurved, flanked

by sharp thorn-like processes of the eighth tergite, found elsewhere only in *antimachus* Drury; female without the pair of triangular processes that flank the ostium postero-laterally in the *cynorta* group. Six species. Tropical Africa. Early stages unknown.

**Section III**

Larva smooth, green, with eye-spots and segmental purple or blue spots; mature larva without saddle; prolegs with an extra row of crochets. Hosts: Lauraceae, Magnoliaceae and various deciduous trees. Adult typically with a median stripe on hind wing, as in Leptocircini. Valve of male ovate, armed with a broad, spoon-like medial clasper, which is coarsely dentate along the distal rim. Two species-groups are usually recognized, although *P. pilumnus* is an almost perfect intermediate between them, having *glaucus*-like maculation, *troilus*-like pupa, and transitional genitalia.[5]

The extra hooks of the prolegs, the lauraceous food-plant, and the presence of a medial stripe on the hind wing all suggest that this group is a very primitive one.

*Glaucus* group: adult normally yellow or white, with black stripes; larva with a narrow transverse line at posterior margin of first abdominal segment; pupa straight and not laterally carinate. Five normal species, to which the transitional *pilumnus* Boisduval is usually added. Range: North America and Mexico.

*Troilus* group: adult dark, with yellow or greenish spots, and in *P. palamedes* Drury with the medial stripe clearly visible on the reverse of the hind wing; larva with a pair of triangular patches on hind margin of first abdominal segment; pupa laterally carinate. Range: North America and Mexico. Two species.

**Section IV**

Adult primitively dark above, with yellow bands and rows of spots, beneath largely yellow; the primitive pattern often greatly modified by mimicry. Valve in primitive forms remarkably like that of Section III, ovate, with medial, spoon-shaped clasper, the rim of which is coarsely or finely dentate. Juxta unique and diagnostic: deeply emarginate, U-shaped or V-shaped, varying little among the species examined. Larva on Rutaceae: mottled brown, with the primitive pale patches yellowish or white, contrasting, and with an ornate band on metathorax and a raised band on the first abdominal segment; the general resemblance to larvae of Section II very striking if the substitution of a brown-and-white for a green-and-brown colouring be allowed for.

There are two subsections, one, comprising the *thoas* group, with the mature larva solitary and lacking tubercles, and the other comprising the *anchisiades* and *torquatus* groups, with the mature larva tuberculate and usually gregarious (but solitary in *hyppason*, according to Moss, 1919).

This section is remarkable for the number of relict species it has in the West Indies. Very likely it is an old Central-American group.

**Subsection A**

Mature larva solitary, without rows of tubercles.

*Thoas* group: the primitive forms of this group are represented by *machaonides* Esper and *andraemon* Hübner, which have normal submarginal lunules and transverse bands. Two lines of evolution are discernible. In one, represented by the series *aristor* Godart, *homothoas* R. and J., *cresphontes* Cramer, the submarginal lunules become thickened, both they and the discal band are displaced basad, and the socii become thorn-like and hypertrophied. In the other line, represented by the series *aristodemus* Esper, *lycophron* Hübner, *androgeus* Cramer, the submarginal lunules remain normal, in the male the discal band becomes progressively broadened, while in the female a dark cryptic or mimetic pattern develops; the socii remain unmodified, but the clasper

[5]See the useful paper by Brower (19??), which has meanwhile appeared.

becomes differentiated into a ventral spine and a dorsal rounded portion bearing a serrated plate.

The larvae of all known species, including the primitive *machaonides* and *andraemon*, are very similar. Food normally Rutaceae, but occasionally Umbelliferae and Piperaceae. About fourteen species. Range: North, Central, and South America and West Indies.

**Subsection B**

Mature larva usually gregarious, always with a pair of dorsal rows of tubercles.

*Anchisiades* group: male and female similar, mimetic or non-mimetic, never with broad yellow bands; Central American and West Indian species predominantly tailed, non-mimetic or mimetic of tailed Troidini (*Battus* spp. and *ascanius* group of *Parides*); South American species tailless, and mimicking *aeneas* and *lysander* groups of *Parides;* clasper rounded and distally dentate or serrate; larvae mostly gregarious, on Rutaceae. About 12 species, Central and South America.

*Torquatus* group: male non-mimetic, black with yellow bands, with rounded primaries and tailed secondaries; female mimetic of *Parides;* larva and genitalia as in previous group. About six species. Neotropical.

**Section V**

Build powerful, costa serrated except in the mimetic *zagreus* group. Frons black or with a median yellow stripe. Male genitalia large and heavily sclerotized; clasper long, free, heavily sclerotized, parallel-sided or gradually tapering, and ending in one or two strong, thorn-like spines, sometimes accompanied by smaller serrations. Larvae so far as known green, with metathoracic eye-spots, transverse band on first abdominal segment and X-shaped saddle. Host plants: Lauraceae and the allied Hernandiaceae.

*Zagreus* group: adult mimetic of Ithomiinae; costal margin not strengthened or serrate; pseuduncus bifid; early stages unknown. Three or four species. Range: Central and South America.

*Scamander* group: costa less strongly dentate than in the following group: larva as described for the Section. Four species. Range: Central and South America. *P. hellanichus* Hewitson, believed by Rothschild and Jordan to be near the stem-form of the Section, has a clasper reminiscent of that of the *zagreus* group.

*Homerus* group: costa strongly serrate; pattern and larva as in *scamander* group. Ten species. Range: Central and South America and Jamaica. It has been suggested to me that *P. homerus* Fabricius is not closely related to the other species of the group, but I can find no foundation for this view. I follow Jordan in regarding *homerus* as a close ally of the continental *P. garamas* Hübner.

**Tribe Troidini**

Troidini Ford, 1944: 213.
Cressidini Ford, 1944: 213.

Tibiae and tarsi with dorsal rows of spines not separated from ventral rows by a spineless, impressed space. Antenna, tibiae and tarsi naked, antenna usually with paired ventral sense-pits on each segment. Male with membrane of wing prominently grooved at 1st A, thence convex to anal margin, this region often with a conspicuous scent organ. Male with ninth and tenth tergites dorsally incomplete; pseuduncus largely intersegmental, usually with dorsal surface unscaled; socii fleshy, coarsely setose, and closely associated with pseuduncus. Female sometimes with a sphragis. Red pigments usually of type A. Larva cylindrical with fleshy, usually red, segmental tubercles, and ordinarily with a white "saddle" on abdominal segments 4 and 5. Pupa with prominent dorso-lateral and lateral pairs of carinae or rows of tubercles. Food-plants Aristolochiaceae, rarely Combretaceae.

The natural divisions of this group are much easier to discern than those of the Papilionini, though there is some difficulty in finding morphological characters to define them. Some of the genera are marked off very sharply, but there is a large central group with essentially uniform structure.

The primitive genera *Euryades* and *Cressida* have the false uncus separated from the eighth tergite by a complete suture. Both of these genera have a well-developed sphragis. That of *Euryades* is bifid and very long; the male has special apodemes that no doubt assist in its production. *Cressida* has an unusually large precostal cell and an unforked, basally directed precosta. The precostal cell of *Euryades* is larger than that of many more specialized troidines, and the precosta is forked, though weakly so. The supposed abortion of the valve of *Cressida* is really no more than a slight narrowing: the valve and clasper are well-developed and rather *Parnassius*-like. There is no doubt that *Euryades* and *Cressida* are directly related: various resemblances are cited by Ford, also Schatz (1892) has pointed out that the two genera have the last segment of the male fore tarsus specialized in the same way; the male genitalia show numerous similarities and the females in both genera have a small, sclerotized bursa copulatrix like that of Zerynthiinae.

Another very distinct genus is *Battus*, as is emphasized by Ford. There the ventral sense-pits of the antenna are lacking and the red pigments are of type B, not of type A as usual in the Troidini. The anal region of the male hind wing has a shiny naked streak instead of a woolly scent-organ, and the larva has some of the thoracic tubercles elongated, instead of having all of the same length.

The remaining Troidini are closely related. Zeuner has shown that the *Troides* and allies are separable from *Parides* and allies by the point of origin of $R_1$, opposite $Cu_2$ in *Troides* and opposite $Cu_1$ in *Parides*. In the *Troides* complex the bursa copulatrix lacks a distinct signum, and transparent golden scales are often present, whereas in *Parides* and allies the signum is present and golden scales are absent.

I follow Zeuner's grouping of the *Troides* complex, except that I reduce *Trogonoptera* to subgeneric rank. In the *Parides* complex the New-World members have a V-shaped signum, the Old-World ones so far as studied a ribbon-like one. The New-World division is very homogeneous. The Old-World one is subdivisible into several entities, distinguished by pattern, type of sex scaling, and details of male genital armature. Of these I am forced to regard *Pachlioptera* as a distinct genus, because of the remarkable structure of the male genitalia, conjoined with recognizable peculairities in the pupa and in the female genitalia. The remaining groups I unite with the New-World forms in the large genus *Parides*.

The larva and pupa of *Cressida* are primitive, having the tubercles low and unspecialized. The larva of *Battus* is specialized, as already noted. The larvae of the remaining groups of Troidini are remarkably uniform, and shed little light on relationships.

Anthoxanthins are preserved in *Euryades* (one species) and in some Neotropical *Parides*. A sphragis is preserved in the same groups and also in *Cressida* and *Trogonoptera*.

### Key to the Genera of Troidini

1. Precosta simple, curved basad ..... *Cressida*
   Precosta forked ..... 2
2. Precosta weakly forked; middle discocellular incurved, much longer than upper discocellular ..... *Euryades*
   Precosta strongly forked; middle discocellular straight or nearly so, usually about the same length as upper discocellular ..... 3
3. Antennal segments with paired ventral pits ..... 4
   Antennal segments without paired ventral pits ..... *Battus*
4. $R_3$ arising opposite $Cu_1$ ..... 5
   $R_3$ arising opposite $Cu_2$ ..... 6
5. Male with valve aborted and socii hypertrophied and sclerotized; female with ductus bursae heavily sclerotized ..... *Pachlioptera*
   Male with valve normal or slightly emarginated; female with ductus bursae membranous ..... *Parides*

6. Male with an eversible area of dense woolly scales on anal field of hind wing; upper and middle discocellulars in line ..... *Troides*
Male without such an area of woolly scales; upper discocellular usually at a decided angle to middle discocellular ..... *Ornithoptera*

### Genus *Euryades* Felder and Felder
### Type-species: *Papilio corethrus* Boisduval

*Euryades* Felder and Felder, 1864: 327.

Tails present or absent. Wing-venation of the type normal in Papilioninae, but with precosta very weakly forked. Hind wing with two complete rows of red spots, red pigment of type A. Anthoxanthins present or absent. Club of antenna curved, ventral sense-hairs sunk in paired pits on each segment. Male with false uncus separated from eighth tergite by a complete suture; valve short, quadrate, posteriorly emarginate; dorsal angles of juxta and anteroventral angles of tegumen prolonged anteriorly into long, ribbon-like apodemes. Female with a prominent, alate sphragis and short, heavily sclerotized bursa. Larva similar to that of *Parides*, according to Burmeister (1878). Hosts: Aristolochiaceae. Two species. Range: temperate South America.

### Genus *Cressida* Swainson
### Type-species: *Cressida heliconides* Swainson

*Cressida* Swainson, 1832-33: 2.
*Eurycus* Boisduval, 1836: 391. Type-species: *Papilio cressida* Fabricius.

Similar to *Euryades*, but with tails and anthoxanthins absent, precosta unforked and directed distad, precostal cell very large, antenna straight, valve narrower, apodemes absent from juxta and tegumen, and sphragis smaller, not alate. Larva *Parides*-like, but with tubercles less prominent than usual in that genus. Pupa with a low dorsal thoracic tubercle and two pairs of abdominal tubercle-rows. Hosts: *Aristolochia* spp. One species, Australia.

### Genus *Parides* Hübner
### Type-species: *Princeps echelus* Hübner

*Parides* Hübner [1819] p. 87.

Similar to *Euryades*, but with precosta strongly forked; udc of primaries usually as long as mdc, mdc usually straight. False uncus often not fully separated from eighth tergite; apodemes absent from juxta and tegumen; sphragis rudimentary or absent; bursa membranous. Larva with well-developed, fleshy, usually pink, segmental tubercles. Pupa with cephalic and thoracic horns and well-marked subdorsal and lateral rows of abdominal tubercles.

The New-World species of this group are uniform in wing-markings and in structure of the male valve, and in having a V-shaped signum. The Old-World species are more diverse, but so far as examined always have a ribbon-like signum. As I have been able to find no other consistent structural difference between New and Old-World species, I consider the difference subgeneric only, particularly as the early stages are similar and the male genitalia of the *latreillei* group are virtually identical with those of the New-World groups. Jordan and Ford both state that the pretarsal sinus is shallower in the New-World species than in those from the Old-World, but in spite of repeated attempts I am unable to perceive this difference.

As several species of the New-World subgenus retain the sphragis and a number retain anthoxanthins, this subgenus is probably more primitive than the Old-World one.

#### Subgenus *Parides* Hübner

*Parides* Hübner [1819] p. 87.
*Hectorides* Hübner, 1821, pl. 318. Type-species: *Papilio agavus* Drury.
*Endopogon* Lacordaire, 1833: 384. Type-species: *Papilio sesostris* Cramer.

*Ascanides* Geyer, 1837: 32. Type-species: *Papilio triopas* Godart.
*Blakea Grote,* 1875: 118. Type-species: *Papilio gundlachianus* Felder.

Signum V-shaped. Valve always rounded and well-developed. Anal region of male always with a white, woolly scent-organ.

The three species-groups distinguished by Jordan seem perfectly natural.

*Ascanius* group: hind wing with submarginal spots, usually also with discal spots or band, mostly with tail; clasper various, but ending in a point or in a finely toothed rounded edge; if ventral edge toothed, the whole clasper narrow; juxta trapezoidal or with sides gently concave; aedoeagus short, humped and bisinuate, expanded at base, resembling that of the *latreillei* group. The retention of submarginal spots, and in some species of tail, sphragis, and anthoxanthins indicate that this group is primitive. Eleven species: Central and South America and Cuba.

*Aeneas* group: hind wing with discal spots or band but without submarginal spots, marginal lunules white; tails usually lacking; clasper of male with one strong ventral tooth or with apico-ventral margin coarsely toothed; juxta strongly vase-shaped or goblet-shaped; aedoeagus comparatively long and slender, usually strongly curved, often with a small expansion at base. Sixteen species: Central and South America.

*Lysander* group: markings as in *aeneas* group, but marginal lunules of hind wing red; clasper broad and triangular with entire or minutely denticulate ventral margin and several coarse apical teeth; juxta more or less trapezoidal; aedoeagus very thick and short, straight or weakly curved. Eight species: Central and South America.

### Subgenus *Atrophaneura* Reakirt
### Type-species: *Atrophaneura erythrosoma* Reakirt

*Atrophaneura* Reakirt, 1864: 446.
*Byasa* Moore, 1882: 258. Type-species: *Papilio philoxenus* G. R. Gray.
*Panosmia* Wood-Mason and de Nicéville, 1886: 374. Type-species: *Papilio dasarada* Moore.
*Pangerana* Moore, 1886: 51. Type-species: *Papilio varuna* White.
*Pharmacophagus* Haase, 1892: 15. Type-species: *Papilio antenor* Drury.
*Karanga* Moore, 1902: 157. Type-species: *Papilio nox* Swainson.
*Losaria* Moore, 1902: 184. Type-species: *Papilio coon* Fabricius.
*Balignina* Moore, 1902: 187. Type-species: *Papilio neptunus* Guérin.

Signum ribbon-like; valve rounded or emarginate; woolly scent-organ present or absent in male. Four species-groups, of which one is doubtfully placed here.

*Antenor* group: antenna not curved; pattern unusually primitive and fully expressed; hind wing tailed; male genitalia like those of *latreillei* group. Female genitalia not examined. Hosts: Combretaceae. One species, Madagascar. Further study may necessitate the removal of this group from *Atrophaneura.*

*Latreillei* group: antenna curved; hind wing long, with spatulate tail and in male with white, woolly scent-organ; valve broadly rounded; aedoeagus stout and knobbed. Fourteen species: Japan and Himalayas to Malaya. An excellent account is given by Jordan (1928).

*Nox* group: tailless or short-tailed; hind wing of male with very broad, rolled-up abdominal fold; valve distally and dorsally emarginate; aedoeagus short and stout. About a dozen species. Range: Sikkim and Formosa to Celebes, mostly insular.

*Coon* group: wings narrow, with petiolate tail; scent-organ of male weakly developed; valve strongly emarginate dorsally; aedoeagus long and slender. Three species: Burma and Andamans to Java.

### Genus *Pachlioptera* Reakirt
### Type-species: *Papilio diphilus* Esper

*Polydorus* Swainson, 1832-33: 100, *nec* Blainville, 1826. Type-species: *Polydorus thoas* Swainson.

*Pachlioptera* Reakirt, 1864: 348.
*Tros* Kirby, 1896: 305. Type-species: *Papilio hector* Linnaeus.

Similar to *Parides*, but male with valve aborted, clasper strong, short and thorn-like, socii and lateral remnants of tegumen hypertrophied and heavily sclerotized, false uncus short and blunt, not marked off from eighth tergite; female ductus bursae heavily sclerotized. Larva as in *Parides*. Pupa with abdominal tubercles developed into prominent longitudinal carinae on each segment. Hosts: Aristolochiaceae.

A closely knit genus of thirteen species. Range: Indo-Australian.

### Genus *Troides* Hübner
### Type-species: *Papilio helena* Linnaeus

*Troides* Hübner [1819] p. 88.

$R_1$ of fore wing arising from cell opposite $Cu_2$; fore wing with wedge-shaped markings along veins; hind wing of male with prominent woolly scent-organ along anal margin. Udc and mdc of fore wing in line, stalk of $R_{+5}$ normally more than half as long as free part of those veins. Male genitalia usually with long, distally spinulose clasper; female without distinct signum, but bursa spinulose, with concentric ovoidal folds. Larva as in *Parides*. Pupa with abdomen much broadened and flattened, subdorsal carinae reduced and very far apart.

The group is primarily Indo-Malayan. There are two subgenera. The species have been well monographed by Zeuner (1943).

#### Subgenus *Troides* Hübner

*Troides* Hübner [1819] p. 88.
*Amphrisius* Swainson, 1833: 98. Type-species: *Amphrisius nymphalides* Swainson.
*Pompeusptera* Rippon, 1889: 9. Type-species: *Papilio helena* Linnaeus. Subsequently emended by Rippon to *Pompeoptera*.

Fore wing with inner margin subequal to outer margin; fore wing mainly black, hind wing with contrasting yellow and black areas. Sphragis absent.

Zeuner (1943: 125) recognizes five species-groups, but three of these can conveniently be considered as subgroups of one major group.

*Helena* group: clasper a long arm with a terminal spiny knob; basal hooks small or absent. Three subgroups: *aeacus* subgroup, five species, Formosa and Siam to Burma; *helena* subgroup, two species, Himalayas to Moluccas; *haliphron* subgroup, five species, Sumatra to Celebes and Timorlaut, with a disjunct species in Ceylon.

*Amphrysus* group: clasper reduced, but with one or both basal hooks very long. Four species, restricted to Borneo, Sumatra, Java, Malaya and neighbouring small islands.

*Hypolitus* group: clasper very short, almost square, without distinct head, and with basal hooks barely indicated. One species, Celebes and Moluccas.

#### Subgenus *Trogonoptera* Rippon

*Trogonoptera* Rippon, 1889: 1. Type-species: *Ornithoptera brookiana* Wallace.

Fore wing with inner margin very short, outer margin long and oblique, almost parallel to costa; hind wing very small. Both wings with green markings, wedge-shaped and contrasting in the male, diffuse in the female. Yellow markings lacking. Valve short and broad, clasper broad and saucer-shaped. Female with sphragis.

Two closely related species. Malacca and Sumatra to Palawan.

### Genus *Ornithoptera* Boisduval
### Type-species: *Papilio priamus* Linnaeus

*Ornithoptera* Boisduval, 1832: 33.
*Priamusptera* Rippon, 1889 [unnumbered page]. Type-species: *Ornithoptera croesus* Wallace. Subsequently emended by Rippon to *Priamoptera*.

*Schoenbergia* Pagenstecher, 1893: 35. Type-species: *Ornithoptera schoenbergi* Pagenstecher.
*Aetheoptera* Rippon, 1894: 47. Type-species: *Ornithoptera victoriae* G. R. Gray.
*Phalaenosoma* Rippon, 1910: 121. Type-species: *Troides chimaera* Rothschild.

Strongly dimorphic: male fore wing with contrasting maculation of metallic green, blue, or orange on a black ground, hind wing with areas of golden scales; female with fore wing black and white, hind wing marked with yellow. Fore wing with ude usually at a considerable angle to mde, stalk of $R_{4+5}$ often very short or lacking. Larva with tubercles longer and more slender than those of *Troides;* pupa smoother and more nearly cylindrical, with all processes small and sharp-pointed.

The genus is primarily Paupan, one species extending to tropical Australia.

The two groups of this genus, as Zeuner points out, differ much less than *Troides* and *Trogonoptera* and I accordingly rank them as species-groups, rather than as subgenera.

A detailed account of the relationships is given by Zeuner.

*Paradisea* group: fore wing of male without a sex-brand. Zeuner's three groups may be recognized as subgroups: *goliath* subgroup, one species, Waigeu, Ceram and New Guinea; *tithonus* subgroup, three species, Waigeu and New Guinea; *paradisea* subgroup, two species, New Guinea.

*Priamus* group: fore wing of male with a lunate sex-brand on the disc. Again I treat Zeuner's species-groups as subgroups: *priamus* subgroup, three species, Moluccas to Australia; *victoriae* subgroup, three species, New Guinea to the Solomons.

## Genus *Battus* Scopoli
## Type-species: *Papilio polydamas* Linnaeus

*Battus* Scopoli, 1777: 433.
*Laertias* Hübner [1819] p. 84. Type-species: *Papilio philenor* Linnaeus.
*Ithobalus* Hübner [1819] p. 88. Type-species: *Papilio polydamas* Linnaeus.
*Pachliopta* Reakirt, 1865: 63. Type-species: *Papilio philenor* Linnaeus.
*Heterocreon* Kirby, 1902: 101. Type-species: *Papilio philenor* Linnaeus.

*Laertiades* Doubleday is an erroneous subsequent spelling of *Laertias* and has no status.

Antenna without ventral pits; anal scent-fold of male hind wing containing sparse black hair bordered by a naked streak; red pigment when present of type B. Male with false uncus closely fused with eighth tergite; valve angulate and proportionally smaller than in *Parides*. Female bursa without a definite signum, but spiculate, with a mid-ventral sinuous seam flanked by ovoid folds. Larva with a pair of very long prothoracic tubercles; anterior and posterior tubercles often considerable longer than those at middle of body.

This genus is very distinct from all others of the tribe. As noted by Ford it shows several resemblances to *Papilio* — absence of antennal sense-pits, presence of red pigment B, and close association of false uncus with eighth tergite — but in my opinion these are the results of convergence and not of immediate relationship.

There are two species groups.

*Philenor* group: adult with a distinct row of submarginal lunules above, at least on hind wing; pupa with length of dorsal thoracic process much less than depth of body. Nine species. Range: North, Central, and South America, and West Indies.

*Belus* group: adult without distinct submarginal lunules on hind wing above, though sometimes with a tapering row of quadrate patches beginning at costa; length of dorsal thoracic horn of pupa equal to depth of body. Five species. Range: Central and South America.

## Summary

The classification of the Papilionidae is reviewed on the basis of evidence from external structure, male and female genitalia, chemistry of pigments, larval characters,

and food-plants. The male genitalia provide important new evidence of relationships, and in particular show the primitive position of the Leptocircini, in which *Teinopalpus* and the Graphiini are included. The arrangement adopted is summarized in the Appendix. It is considerably modified from the latest published arrangement, that of Ford (1944 a), and is presented in much greater detail. One new genus, *Protographium*, type-species *Papilio leosthenes* Doubleday, is described.

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## APPENDIX
### Taxonomic Disposition of Species of Papilionidae

Subfamily Baroniinae
Genus *Baronia* Salvin
*brevicornis* Salvin
Subfamily Parnassiinae
Tribe Parnassiini
Genus *Archon* Hübner
*apollinus* (Herbst)
Genus *Hypermnestra* Ménétriés
*helios* (Nickerl)
Genus *Parnassius* Fabricius
Subgenus *Parnassius* Fabricius
*apollo* group
*apollonius* (Eversmann), *honrathi* Staudinger and Bang-Haas, *bremeri* Bremer, *phoebus* (Fabricius), *actius* (Eversmann), *jacquemontii* Boisduval, *epaphus* Oberthür, *tianschanicus* Oberthür, *nomion* (Hübner), *apollo* (Linnaeus)
Subgenus *Doritis* Fabricius
*mnemosyne* group
*mnemosyne* (Linnaeus), *stubbendorfi* Ménétriés, *eversmanni* Ménétriés, *nordmanni* Ménétriés, *clarius* Eversmann, *clodius* Ménétriés, *orleans* Oberthür
*hardwickei* group
*hardwickei* Gray
*szechenyii* group
*szechenyii* Frivaldszky, *cephalus* Grum-Grshimailo, *pythia* Roth
*acco* group
*acco* Gray, *przewalskii* Alpheraky, *rothschildianus* Bryk, *hannyngtoni* Avinoff, *maharaja* Avinoff
*delphius* group
*patricius* Niepelt, *acdestis* Grum-Grshimailo, *delphius* (Eversmann), *stoliczkanus* C. and R. Felder, *stenosemus* Honrath
*imperator* group
*imperator* Oberthür
*charltonius* group
*charltonius* Gray, *inopinatus* Kotzsch, *loxias* Püngeler
*tenedius* group
*tenedius* Eversmann
*simo* group
*simo* Gray
Tribe Zerynthiini
Genus *Allancastria* Bryk
*cerisyi* (Godart)
Genus *Serecinus* Westwood
*telamon* (Donovan)
Genus *Zerynthia* Ochsenheimer
*hypermnestra* (Scopoli), *rumina* (Linnaeus)
Genus *Luehdorfia* Crüger
*puziloi* (Erschoff), *japonica* Leech, ? *bosniackii* (Rebel)
Genus *Bhutanitis* Atkinson
*thaidina* (Blanchard), *lidderdalei* Atkinson, *mansfieldi* Riley, *ludlowi* Gabriel

Subfamily Papilioninae
Tribe Leptocircini
Genus *Lamproptera* G. R. Gray
*curius* (Fabricius), *meges* (Zinken)
Genus *Teinopalpus* Hope
*imperialis* Hope, *aureus* Mell
Genus *Eurytides* Hübner
Subgenus *Protesilaus* Swainson
Section I
*marcellus* group
*marcellus* (Cramer), *marcellinus* (Doubleday), *celadon* (Lucas), *zonaria* (Butler), *philolaus* (Boisduval), *xanticles* (Bates), *oberthuri* (Rothschild and Jordan), *arcesilaus* (Lucas), *epidaus* (Doubleday), *bellerephon* (Dalman)
*lysithous* group
*pausanias* (Hewitson), *protodamas* (Godart), *microdamas* (Burmeister), *phaon* (Boisduval), *chibeha* (Fassl), *euryleon* (Hewitson), *hipparchus* (Staudinger), *harmodius* (Doubleday), *trapeza* (Rothschild and Jordan), *xynias* (Hewitson), *ariarathes* (Esper), *ilus* (Fabricius), *branchus* (Doubleday), *belesis* (Bates), *thymbraeus* (Boisduval), *lysithous* (Hübner), *kumbachi* (Vogeler), *asius* (Fabricius)
Section II
*protesilaus* group
*agesilaus* (Guerin and Percheron), *glaucolaus* (Bates), *molops* (Rothschild and Jordan), *protesilaus* (Linnaeus), *helios* (Rothschild and Jordan), *orthosilaus* (Weymer), *stenodesmus* (Rothschild and Jordan), *earis* (Rothschild and Jordan), *telesilaus* (Felder), *embrikstrandi* (d'Almeida), *travassosi* (d'Almeida)
Subgenus *Eurytides* Hübner
*thyastes* group
*marchandi* (Boisduval), *thyastes* (Drury), *dioxippus* (Hewitson), *lacandones* (Bates), *calliste* (Bates), *leucaspis* (Godart)
*dolicaon* group
*servillei* (Godart), *columbus* (Kollar), *orabilis* (Butler), *salvini* (Bates), *callias* (Rothschild and Jordan), *dolicaon* (Cramer), *iphitas* Hübner
Genus *Protographium*, novum
*leosthenes* (Doubleday)
Genus *Iphiclides* Hübner
*podalirius* (Linnaeus), *podalirinus* (Oberthür)
Genus *Graphium* Scopoli
Subgenus *Graphium* Scopoli
*codrus* group
*macleayanus* (Leach), *weiskei* (Ribbe), *codrus* (Cramer), *empedocles* (Fabricius), *cloanthus* (Westwood), *sarpedon* (Linnaeus), *protensor* (Gistel), *gelon* (Boisduval)
*eurypylus* group
*doson* (Felder), *evemon* (Boisduval), *eurypylus* (Linnaeus), ? *procles* (Grose-Smith), ? *meyeri* (Hopffer), *bathycles* (Zinken), *leechi* (Rothschild), ? *macfarlanei* (Butler), *mendana* (Godman and Salvin), *arycles* (Boisduval)
*agamemnon* group
*agamemnon* (Linnaeus), ?*meeki* (Rothschild)

*wallacei* group
*wallacei* (Hewitson), *browni* (Godman and Salvin), *hicateon* (Mathew)
Subgenus *Arisbe* Hübner
*antheus* group
*antheus* (Cramer), *evombar* (Boisduval)
*porthaon* group
*porthaon* (Hewitson)
*colonna* group
*colonna* (Ward)
*policenes* group
*policenes* (Cramer), *nigrescens* (Eimer), *junodi* (Trimen), *sisenna* (Mabille), ?*boolae* (Strand)
*illyris* group
*illyris* (Hewitson), *gudenusi* (Rebel), *kirbyi* (Hewitson)
*philonoe* group
*philonoe* (Ward)
*leonidas* group
*cyrnus* (Boisduval), *leonidas* (Fabricius), *levassori* (Oberthür)
*ucalegon* group
*hachei* (Dewitz), *auriger* (Butler), *ucalegon* (Hewitson), *simoni* (Aurivillius), *fulleri* (Grose-Smith), *ucalegonides* (Staudinger), *almansor* (Honrath), *odin* (Strand), *olbrechtsi* (Berger), *aurivilliusi* (Seeldrayers), *agamedes* (Westwood), *adamastor* (Boisduval)
*tyndaraeus* group
*tyndaraeus* (Fabricius), *latreilliamus* (Godart)
*pylades* group
*endochus* (Boisduval), *taboramus* (Oberthür), *morania* (Angas), *pylades* (Fabricius), *ridleyanus* (White)

Subgenus *Pathysa* Reakirt
*antiphates* group
*agetes* (Westwood), *stratiotes* (Grose-Smith), *nomius* (Esper), *aristeus* (Cramer), *rhesus* (Boisduval), *dorcus* (de Haan), *androcles* (Boisduval), *antiphates* (Cramer), *euphrates* (Felder)
*macareus* group
*phidias* (Oberthür), *macareus* (Godart), *xenocles* (Doubleday), *leucothoe* (Westwood), *delesserti* (Guerin), *megarus* (Westwood), *megaera* (Staudinger), *stratocles* (Felder), *deucalion* (Boisduval), *thule* (Wallace), *idaeoides* (Hewitson), *encelades* (Boisduval)
*eurous* group
*eurous* (Leech), *mandarinus* (Oberthür), *alebion* (G. R. Gray), and *tamerlanus* (Oberthür)
Genus *Dabasa* Moore
*gyas* (Westwood), *payeni* (Boisduval)

Tribe Papilionini
Genus *Papilio* Linnaeus
Section I

*agestor* group
*agestor* (G. R. Gray), *epicydes* (Hewitson), *slateri* (G. R. Gray)

*clytia* group
*clytia* Linnaeus, *paradoxa* Zinken
*veiovis* group
*veiovis* Hewitson
*laglaizei* group
*laglaizei* Depuiset, *toboroi* Ribbe, *moerneri* Aurivillius

Section II
Subsection A
Series I
*aegeus* group
*aegeus* Donovan, *bridgei* Mathew, ?*tydeus* Felder, ?*heringi* Niepelt, ?*weymeri* Niepelt, ?*gambrisius* Cramer, ?*inopinatus* Butler, ?*oberon* Grose-Smith
*godeffroyi* group
*godeffroyi* Semper, *schmeltzi* Herrich-Schäffer, ?*amynthor* Boisduval
*woodfordi* group
*woodfordi* Godman and Salvin, ?*ptolychus* Godman and Salvin, ?*erskinei* Mathew
*fuscus* group
*fuscus* Goeze, *canopus* Westwood, ?*diophantus* Grose-Smith, ?*antonio* Hewitson, ?*noblei* de Nicéville, ?*albinus* Wallace, ?*hipponous* Felder, ?*sakontala* Hewitson, ?*jordani* Fruhstorfer, ?*walkeri* Janson
*castor* group
*castor* Westwood, *dravidarum* Wood-Mason
*polytes* group
*polytes* Linnaeus, *ambrax* Boisduval, *phestus* Guérin
*helenus* group
*helenus* Linnaeus, *sataspes* Felder, *iswara* White, *iswaroides* Fruhstorfer, *chaon* Westwood, *nubilus* Staudinger, *nephelus* Boisduval
*memnon* group
*ascalaphus* Boisduval, *oenomaus* Godart, *polymnestor* Cramer, *lampsacus* Boisduval, *forbesi* Grose-Smith, *acheron* Grose-Smith, *mayo* Atkinson, *lowi* Druce, *memnon* Linnaeus, *rumanzovia* Eschscholtz, *deiphobus* Linnaeus
*protenor* group
*protenor* Cramer, ?*demetrius* Cramer, ?*alcmenor* Felder, ?*thaiwanus* Rothschild
*bootes* group
*janaka* Moore, *bootes* Westwood, *elwesi* Leech
*demolion* group
*demolion* Cramer, *liomedon* Moore, *gigon* Felder, *euchenor* Guérin, *menestheus* Drury, *lormieri* Distant, *ophidicephalus* Oberthür
*demoleus* group
*demoleus* Linnaeus, *demodocus* Esper, *erithonioides* Grose-Smith, *morondavana* Grose-Smith, *grosesmithi* Rothschild
*xuthus* group
*xuthus* Linnaeus
*machaon* group
*alexanor* Esper, *hospiton* Guenee, *machaon* Linnaeus, *hippocrates* Felder, *oregonia* Edwards, *zelicaon* Lucas, *bairdi* Edwards, *nitra* Edwards, *polyxenes* Fabricius, *brevicauda* Saunders, *indra* Reakirt

Series 2

*paris* group

*bianor* Cramer, *polyctor* Boisduval, *paris* Linnaeus, *karna* C. and L. Felder, *arcturus* Westwood, *hoppo* Matsumura, *elphenor* Doubleday, *dialis* Leech,

*palinurus* group

*krishna* Moore, *crino* Fabricius, *buddha* Westwood, *palinurus* Fabricius, *blumei* Boisduval

*peranthus* group

*neumoegeni* Honrath, *peranthus* Fabricius, *lorquinianus* Felder, *pericles* Wallace

*ulysses* group

*ulysses* Linnaeus, *montrouzieri* Boisduval

Subsection B

*zalmoxis* group

*zalmoxis* Hewitson

*antimachus* group

*antimachus* Drury

*rex* group

*rex* Oberthür

*phorcas* group

*dardanus* Brown, *constantinus* Ward, *nandina* Rothschild, *phorcas* Cramer, *nobilis* Rogenhofer, *euphranor* Trimen, *pe'odorus* Butler, *hesperus* Westwood

*cynorta* group

*cynorta* Fabricius, *plagiatus* Aurivillius, *echerioides* Trimen, *zoroastres* Druce, *jacksoni* Sharpe, *fulleborni* Karsch, *sjoestedti* Aurivillius

*nireus* group

*mackinnoni* Sharpe, *charopus* Westwood, *hornimani* Distant, *sosia* Rothschild, *aethiops* Rothschild and Jordan, *oribazus* Boisduval, *brontes* Godman, *bromius* Doubleday, *thuraui* Karsch, *nireus* Linnaeus, *manlius* Fabricius, *epiphorbas* Boisduval, *phorbanta* Linnaeus

*delalandei* group

*delalandei* Godart, *mangoura* Hewitson

*leucotaenia* group

*leucotaenia* Rothschild

*gallienus* group

*mechowi* Dewitz, *gallienus* Aurivillius, *zenobius* Godart, *mechowianus* Dewitz, *andronicus* Ward, *zenobia* Fabricius

Section III

*glaucus* group

*glaucus* Linnaeus, *rutulus* Lucas, *multicaudatus* Kirby, *eurymedon* Lucas, *alexiares* Hopffer, *?pilumnus* Boisduval

*troilus* group

*troilus* Linnaeus, *palamedes* Drury

Section IV

Subsection A

*thoas* group

*andraemon* Hübner, *machaonides* Esper, *ornythion* Boisduval, *lycophron* Hübner, *thersites* Fabricius, *androgeus* Cramer, *aristor*

Godart, *caiguanabus* Poey, *aristodemus* Esper, *paeon* Boisduval, *homothoas* Rothschild and Jordan, *thoas* Linnaeus, *cresphontes* Cramer

Subsection B

*anchisiades* group

*hyppason* Cramer, *pelaus* Fabricius, *oxynius* (Hübner), *epenetus* Westwood, *chiansiades* Westwood, *pharnaces* Doubleday, *erostratus* Westwood, *rogeri* Boisduval, *anchisiades* Esper, *maroni* Moreau, *isidorus* Doubleday, *rhodostictus* Butler and Druce, *erostratinus* Vazquez

*torquatus* group

*himeros* Hopffer, *lamarchei* Staudinger, *hectorides* Esper, *garleppi* Staudinger, *torquatus* Cramer, *tasso* Staudinger, *peleides* Esper

Section V

*zagreus* group

*zagreus* Doubleday, *neyi* Niepelt, *ascolius* Felder, *bachus* Felder

*scamander* group

*hellanichus* Hewitson, *scamander* Boisduval, *birchalli* Hewitson, *xanthopleura* Godman and Salvin

*homerus* group

*victorinus* Doubleday, *cephalus* Godman and Salvin, *cleotas* Gray, *aristeus* Cramer, *judicael* Oberthür, *garamas* (Hübner), *homerus* Fabricius, *warscewiczi* Hopffer, *cacicus* Lucas, *euterpinus* Godman and Salvin

Tribe Troidini

Genus *Euryades* Felder and Felder

*corethrus* (Boisduval), *duponchelii* Lucas

Genus *Cressida* Swainson

*cressida* (Fabricius)

Genus *Parides* Hübner

Subgenus *Parides* Hübner

*ascanius* group

*gundlachianus* (Felder,) *ascanius* (Cramer), *agavus* (Drury), *proneus* (Hübner), *chamissonia* (Eschscholtz), *perrhebus* (Boisduval), *phalaecus* (Hewitson), *photinus* (Doubleday), *alopius* (Godman and Salvin), *dares* (Hewitson), *montezuma* (Westwood)

*aeneas* group

*hahneli* (Staudinger), *triopas* (Godart), *chabrias* (Hewitson, *coelus* (Boisduval), *quadratus* (Staudinger), *pizzaro* (Staudinger), *steinbachi* (Rothschild), *klagesi* (Ehrmann), *aeneas* (Linnaeus), *schuppi* (Röber), *tros* (Fabricius), *orellana* (Hewitson), *sesostris* (Cramer), *childrenae* (Gray), *erlaces* (Gray), *burchellanus* (Westwood), *drucei* (Butler), *cutorina* (Staudinger), *phosphorus* (Bates), *vertumnus* (Cramer), *lycimenes* (Boisduval), *erithalion* (Boisduval), *polyzelus* (Felder), *iphidamas* (Fabricius), *anchises* (Linnaeus), *nephalion* (Godart), *eversmanni* (Ehrmann)

*lysander* group

*panthonus* (Cramer), *aglaope* (Gray), *lysander* (Cramer), *echemon* (Hübner), *neophilus* (Hübner), *zacynthus* (Fabricius), *arcas* (Cramer), *timias* (Gray)

Subgenus *Atrophaneura* Reakirt

*antenor* group
*antenor* (Drury)
*latreillei* group
*polla* (de Nicéville), *latreillei* (Donovan), *philexonus* (Gray), *dasarada* (Moore), *hedistus* (Jordan), *crassipes* (Oberthür), *daemonius* (Alpheraky), *adamsoni* (Grose-Smith), *nevilli* (Wood-Mason), *laos* (Riley and Godfrey), *mencius* (Felder), *impediens* (Rothschild), *plutonius* (Oberthür), *alcinous* (Klug)
*nox* group
*semperi* (Felder), *dixoni* (Grose-Smith), *kuhni* (Honrath), *priapus* (Boisduval), *sycorax* (Grose-Smith), *hageni* (Rogenhofer), *aidoneus* (Doubleday), *sauteri* (Heyne), *varuna* (White), *zaleucus* (Hewitson), *nox* (Swainson), *luchti* (Roepke)
*coon* group
*neptunus* (Guérin), *coon* (Fabricius), *rhodifer* (Butler)

Genus *Pachlioptera* Reakirt
*hector* (Linnaeus), *jophon* (Gray), *pandiyana* (Moore), *oreon* (Doherty), *liris* (Godart), *polyphontes* (Boisduval), *polydorus* (Linnaeus), *aristolochiae* (Fabricius), *strandi* (Bryk), *mariae* (Semper), *phegeus* (Hopffer), *schadenbergi* (Semper), *atropos* (Staudinger)

Genus *Troides* Hübner
Subgenus *Troides* Hübner
*helena* group
*aeacus* subgroup
*prattorum* (Joicey and Talbot), *magellanus* (Felder), *rhadamantus* (Lucas), *aeacus* (Felder), *minos* (Cramer)
*helena* subgroup
*helena* (Linnaeus), *oblongomaculatus* (Goeze)
*haliphron* subgroup
*darsius* (Gray), *vandepolli* (Snellen), *criton* (Felder), *riedeli* (Kirsch), *haliphron* (Boisduval)
*amphrysus* group
*andromache* (Staudinger), *mirandus* (Butler), *cuneifer* (Rothschild), *amphrysus* (Cramer)
*hypolitus* group
*hypolitus* (Cramer)
Subgenus *Trogonoptera* Rippon
*brookiana* (Wallace), *trojana* (Staudinger)

Genus *Ornithoptera* Boisduval
*paradisea* group
*goliath* subgroup
*goliath* Oberthür
*tithonus* subgroup
*tithonus* de Haan, *chimaera* (Rothschild), *rothschildi* (Kenrick)
*paradisea* subgroup
*paradisea* Staudinger, *meridionalis* (Rothschild)
*priamus* group
*priamus* subgroup
*priamus* (Linnaeus), *croesus* Wallace, *aesacus* (Ney)

*victoriae* subgroup

*victoriae* Gray, *alexandrae* (Rothschild), *allottei* (Rothschild)

Genus *Battus* Scopoli

*philenor* group

*philenor* (Linnaeus), *devilliersi* (Godart), *zetes* (Westwood), *streckerianus* (Honrath), *archidamas* (Boisduval), *polydamas* (Linnaeus), *philetas* (Hewitson), *madyes* (Doubleday), *polystictus* (Butler)

*belus* group

*eracon* (Godman and Salvin), *belus* (Cramer), *laodamas* (Felder), *lycidas* (Cramer), *crassus* (Cramer)

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